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August 23–27, 1999

Sélection de travaux du

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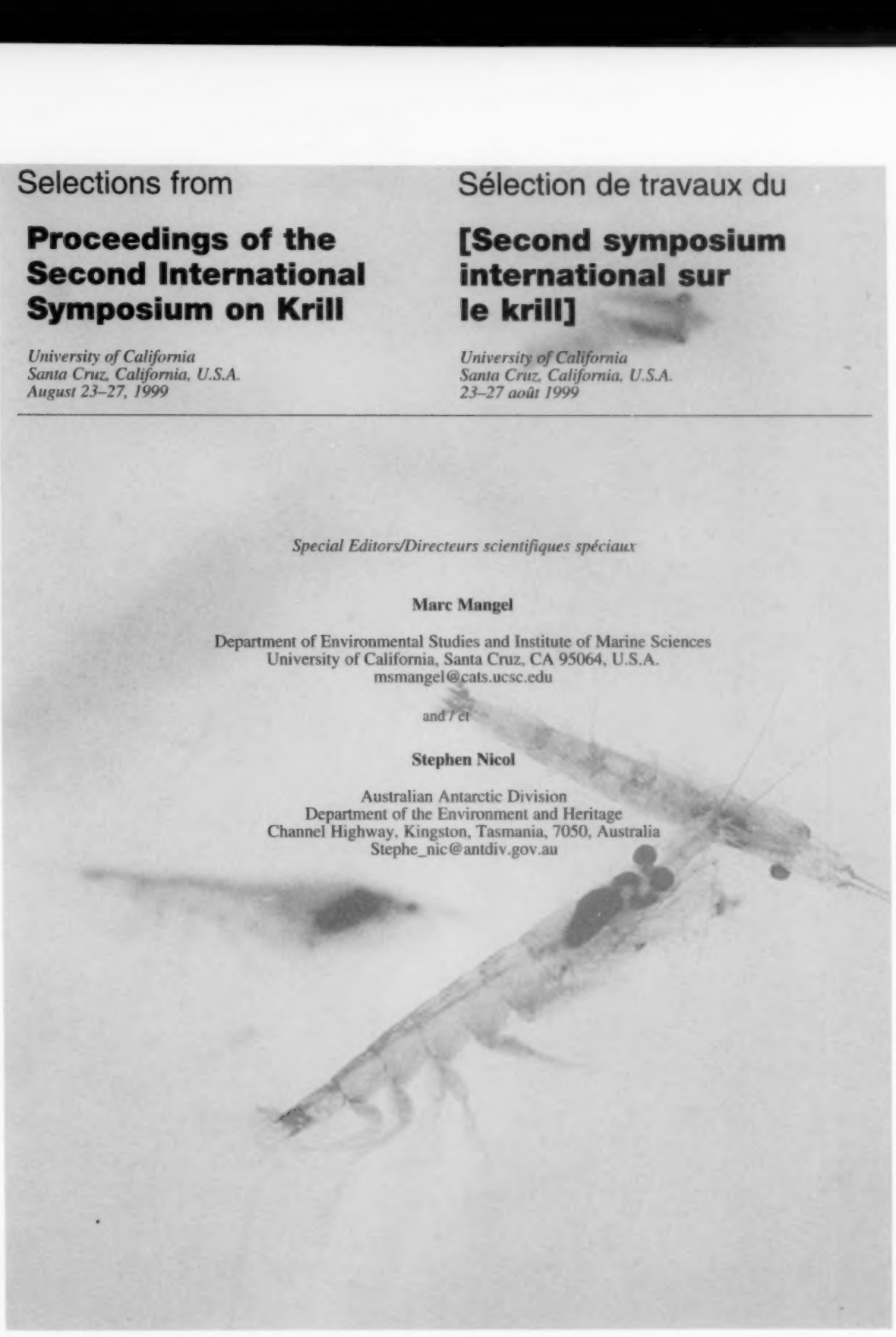

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Krill and the unity of biology

Marc Mangel and Stephen Nicol

Abstract: This supplement features some of the printed papers from the Second International Symposium on Krill (Santa Cruz, Calif., August 1999). Krill have long been recognized as key prey species for fish, birds, and marine mammals and as a target for fisheries in both hemispheres. However, the study of krill can contribute in many other areas of biology. Krill are an excellent model system for studies of growth and maturity, for connections between theory, experiment, and observation, and for tests of evolutionary theory in the field. Krill are also ideal model organisms for studying the interaction between environmental and organismal variability. Because they are widely distributed but only moderately speciose, the study of krill can also shed light on the relationship between abundance and range. The study of krill is an inherently interdisciplinary field, crossing boundaries and using a combination of oceanography, biochemistry, physiology, evolution, and ecology to understand krill and their role in the ecosystem.

Résumé : Ce supplément contient les textes de certaines présentations faites au Second symposium international sur le krill (Second International Symposium on Krill) tenu à Santa Cruz, Calif., en août 1999. Depuis longtemps, on sait que les espèces du krill sont des proies essentielles pour les poissons, les oiseaux et les mammifères marins et une ressource convoitée par les pêches commerciales dans les deux hémisphères. L'étude du krill peut aussi faire progresser plusieurs disciplines biologiques. C'est un système idéal pour analyser la croissance et la maturité, pour évaluer les rapports entre la théorie, l'expérimentation et l'observation, ainsi que pour élaborer en nature des tests relatifs à la théorie de l'évolution. Les organismes qui le composent sont aussi d'excellents modèles pour mettre en lumière les interactions entre la variabilité de l'environnement et celle des organismes. Parce que le krill a une répartition géographique étendue et une richesse en espèces moyenne, il permet l'étude des relations entre l'abondance et l'aire de distribution. Il s'agit essentiellement d'un domaine de recherche interdisciplinaire qui, à l'aide de l'océanographie, de la biochimie, de la physiologie, de la biologie évolutive et de l'écologie, cherche à comprendre la nature du krill et son rôle dans l'écosystème.

[Traduit par la Rédaction]

Introduction

The papers in this supplement are the written versions of some of the presentations at the Second International Symposium on Krill held at the University of California Santa Cruz in August 1999. The First International Krill Symposium (George 1984) was held in Wilmington, N.C., in 1982 and focused on Antarctic krill (*Euphausia superba*). The second, 17 years later, included all species and covered a wider range of topics (Table 1).

The purpose of the symposium was to review current knowledge of krill (euphausiid) biology, to highlight gaps and future areas for research, and to show how the study of a range species of krill can illuminate more general problems (e.g., krill flux, recruitment, swarming behaviour, age, and growth). Here, we summarize the contents in a manner that shows how the study of krill can contribute greatly to our understanding of biology.

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Conservation biology: krill are important

A number of superlatives have been attached to krill, particularly Antarctic krill; they are among the world's most abundant metazoan species (Nicol 1994), they are recorded as forming the largest aggregation of marine life (Macauley et al. 1984), they have the most powerful proteolytic enzymes yet found (Anheller et al. 1989), and they may have a great untapped fisheries potential (Nicol and Endo 1997). Krill (especially the southern ocean krill *E. superba*) are central to pelagic marine food webs, in the sense that most organisms are either directly predators of krill or are just one trophic level removed from krill. For this reason alone, the conservation biology of krill will always be a timely and important subject, since conservation biology provides the scientific context for policy decisions. Furthermore, as fisheries for krill continue to develop (e.g., Nicol and Endo 1997), they will require more detailed information on the life history and ecology of the target species. Good fisheries management is underlain by good science; the study of krill contributes to the management of krill fisheries, and many of the papers in this supplement have their genesis in the quest for information to assist management.

Because of the central role of krill in marine ecosystems, innovative approaches to the management of harvesting of krill have developed in the last 20 years. Agreements such as

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Table 1. Comparison of topics and approaches at the first (1982) and second (1999) symposia on krill.

Topic	No. of papers	No. of experimental studies
1999		
Oceanography	11	
Acoustics	4	
Demography	6	
Schooling/swarming	5	1
Feeding	7	3
Respiration/excretion/metabolism		
Energetics/physiology	4	3
Genetics	3	
Development/growth	7	6
Vertical distribution	5	1
Lipids	8	
Enzymes	3	
Parasites	2	1
Behaviour	2	1
Swimming	1	1
Aging		
Life history	1	
Modelling	1	
Reproduction	4	2
UV	1	
Larvae	2	
1982		
Oceanography	2	
Acoustics	1	
Demography	2	
Schooling/swarming	3	1
Feeding	4	3
Respiration/excretion/metabolism	3	2
Energetics	1	
Genetics	1	
Development/growth	1	1
Vertical distribution	1	
Lipids	1	
Aging	1	

the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), emphasizing an "ecosystem approach," have pushed marine resource management into new areas, both scientifically and politically. The study of krill forces one to take an ecosystem perspective. Only now, 20 years after CCAMLR was negotiated, are other management bodies coming to grips with issues such as ecologically sustainable development and the precautionary approach — ideas that were pioneered by CCAMLR and that have been applied in the management of the Antarctic krill fishery.

Krill as a model system

Krill have proved to be quite good experimental animals (Nicol 2000), informative of basic biology as well as krill-specific problems. They are more robust than many pelagic organisms and can survive quite well in captivity. They pass through a broad size range in their life cycle. For example, *E. superba* larvae are planktonic at 2–3 mm long, yet the adults are truly micronektonic at up to 60 mm long. As adults, they are of a size that makes them good candidates for laboratory research. They can be maintained in large numbers, yet are large enough to be individually manipulated. Because of their large size as adults, their biochemistry and physiology can be examined in detail, even at the level of individual organs.

Understanding the linkage across different levels of biological organization will continue to be one of the great challenges in biology in the new century. The basic principle is that the structure of the organism constrains the response to natural selection and that natural selection acts on the structure of the organism. For example, krill use lipids for both reproduction and dealing with periods of food shortage. The different krill species allocate and use the different lipids (e.g., wax esters and triglycerides) in different ways and show different winter reductions in metabolic rates (Cuzin-Roudy 2000). It should be possible to understand the patterns of allocation in terms of the timing of reproduction (e.g., the spring plankton bloom) and food availability over the winter (Virtue et al. 2000). Falk-Petersen et al. (2000) suggests that lipid biochemistry is a crucial force in speciation, since different lipid biochemistries will lead to different patterns of allocation, use, and reproduction. These may ultimately lead to reproductive isolation, and thus, krill can be used for study of sympatric speciation in open systems.

Krill also allow us to take evolutionary thinking back into the field. For example, it is proposed that some of the pelagic teleost fish have evolved large egg size as an anti-predator mechanism because krill are a plentiful and voracious predator (Y. Hirano, Port of Nagoya Public Aquarium, Nagoya, Japan, personal communication). This hypothesis suggests a clear field experiment, especially suitable for a project such as Southern Ocean GLOBEC.

Krill of many species form dense and extensive swarms and schools (Hamner and Hamner 2000). These aggregations provide model systems for studying the evolutionary and behavioural ecology of group formation. Here, the great challenge is to understand what causes optimal group size (Fig. 1), what sets the limit on evolutionarily stable group size, and what prevents large groups from splintering (Ritz 2000). Krill aggregations also provide challenges for the study of marine ecology; because of their size and their density, they can have major modifying effects on their local environment. The study of the relationship between aggregations of krill, the local oceanographic characteristics, and water movements will also provide insights into how pelagic organisms cope with a fluid environment and, on a larger scale, into the study of marine biogeography.

Finally, the study of krill can provide considerable insight into questions concerning aging and maturity. Krill show what might be considered "standard" patterns of aging, with increasing mortality rates at later ages (Fig. 2), but their patterns of maturation and reproduction are exceedingly complex. Indeed, krill are an ideal study species (Cuzin-Roudy 1993, 2000) to show that maturation and reproduction are coupled but distinct processes. For example, in Antarctic krill, the reproductive cycle involves 10 stages; eight of these lead to ovarian development and egg production and two to sexual regression and reorganization after spawning

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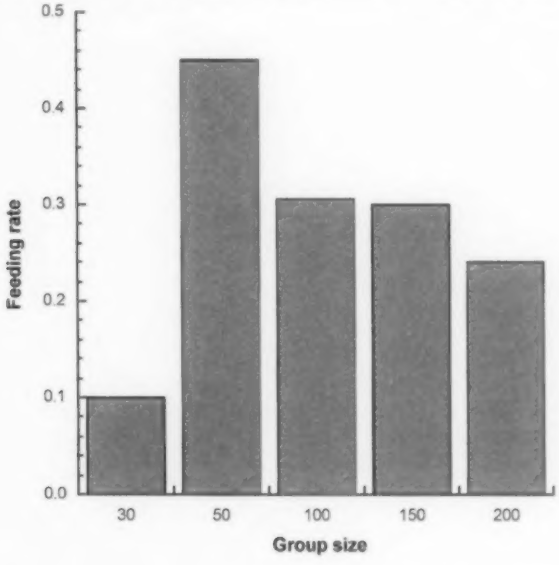
Fig. 1. Feeding rate in groups of hypothetical euphausiids. The optimal group size is that which provides the highest feeding rate. The evolutionarily stable group size is that which provides the same feeding rate as a single individual. Study of krill group formation will allow us a deeper understanding of the origins and maintenance of optimal and evolutionarily stable group size.



periods. Different species of krill have adapted their reproductive cycles for the different habitats in which they are found through physiological flexibility in gonad development (Cuzin-Roudy 1993, 2000). That is, maturation can occur in the absence of reproduction, with profound implications for how we view the connections between growth rate, mortality rate, size, and maturity (Stamps et al. 1998).

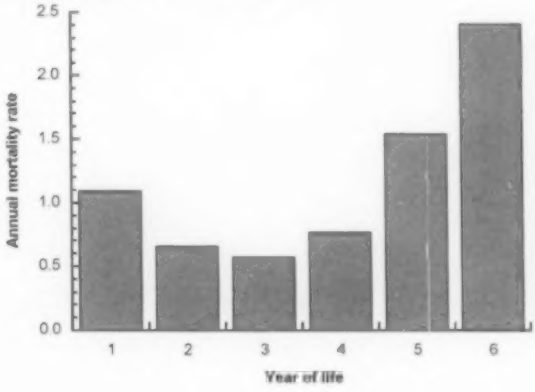
Variability

Krill are also ideal model organisms for studying the interaction between environmental and organismal variability (Siegel 2000*a*, 2000*b*). Krill face variation and uncertainty on a number of scales: (*i*) unpredictable short-term variation, (*ii*) seasonal meso- and large-scale variation, (*iii*) interannual variability, and (*iv*) regime shifts. Biological variation is not noise; indeed, "variation is the core of biology" (Berry 1989). The studies of krill swarms, schools, and aggregations and their causes and response to environmental variation will surely increase our understanding of biological variability and will lead to the recognition that organisms are variable, do have variable responses to the environment, and that much of this variation can be understood.

Krill and the fundamental problem of ecology

In a very real sense, understanding the relationship between abundance and range is the fundamental problem of ecology (Ney-Nifle and Mangel 2000), and krill are an ideal organism for understanding this problem. The euphausiids are enormously successful, with a worldwide distribution but

Fig. 2. Annual mortality rate of krill as a function of year of life showing the standard pattern of increasing mortality with increasing age (based on Pakhomov 1995).



not speciose. Understanding the causes of their success and wide-ranging distributions will thus allow us deeper understanding of the fundamental problem of ecology (Jarman et al. 2000).

But this understanding will require methodological development. Quantifying the abundance and defining the range of pelagic animals such as krill are fraught with problems. All too often the results of ecological investigations depend on the tools used to study and collect the organisms in question. This problem has long been recognized in marine biology, and in his classic monograph on krill, Marr (1962) lamented that "for too long we have been putting too much trust in what seems to be revealed by apparatus, and not enough in what we can actually see." Hamner and Hamner (2000) muse on the mismatch between the observations of density in krill schools and the density estimated by echosounders and ponder why the echosounders are believed and the observations ignored. The problems of estimating krill abundance were acknowledged at the first krill symposium in 1982, and the mismatches between visually observed densities and those estimated by nets and by echosounders, which themselves fail to agree, remain. Even more confounding are the differences between the estimates of krill consumption by predators and the estimates of krill abundance obtained from acoustic surveys. We look forward to the solution of this problem.

Links between theory and observation

Marine science is a global science, and of all the biological sciences, it was among the earliest to recognize the importance of theory and quantitative methods (Smith 1994; Quinn and Deriso 1999). The study of krill provides excellent opportunities to link theory and observation in the field or laboratory. Observation raises questions, structures models, and provides parameters. Theory, which allows us to move beyond the data (Peters 1992), complements observation by providing predictions and leading to deeper understanding.

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Conclusion

The papers in this supplement provide evidence of the vibrancy of the field of krill research, with evidence of theoretical developments (Tarling et al. 2000), field research (Brierley and Watkins 2000; Cripps and Atkinson 2000; Nicol 2000; Pakhomov 2000; Zane and Patarnello 2000), and laboratory investigations (Buchholz and Saborowski 2000; Mayzaud et al. 2000; Nicol 2000). The study of krill is an inherently interdisciplinary field, crossing boundaries and using a combination of oceanography, biochemistry, physiology, evolution, and ecology to understand krill and its role in the ecosystem. Participants at the symposium came from 17 different countries, and a wide range of species from various ocean regions were discussed, illustrating the global importance of krill. Understanding of the biology and ecology of krill has advanced markedly since the first krill symposium in 1982, but there was a definite feeling that theoretical and practical tools were improving at such a rate that it would be unwise to wait another 17 years before the next symposium.

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Seasonal reproduction, multiple spawning, and fecundity in northern krill, *Meganyctiphanes norvegica*, and Antarctic krill, *Euphausia superba*

Janine Cuzin-Roudy

Abstract: Both northern krill, *Meganyctiphanes norvegica*, and Antarctic krill, *Euphausia superba*, release eggs seasonally in multiple spawning events. Fecundity estimates were determined based on counts of mature oocytes in the ovary of females in preserved field samples. Principal components analysis and allometry were used to analyze the covariation of egg-batch size with female characteristics. In both krill species, egg-batch size scaled isometrically with ovarian weight but showed a positive allometry with body size. Predicted egg-batch size ranged from 200 to 4000 eggs for *M. norvegica* of 25.5–35 mm body length and from 1500 to 6000 eggs for *E. superba* of 36–55 mm. Allometric relationships can be used to predict annual fecundity from size structure data of krill populations. In this study, the effect of temperature on the duration of molting and spawning cycles was used to infer a number of reproductive cycles per year, taking into account climate and seasonal variation.

Résumé : Chez le krill nordique, *Meganyctiphanes norvegica*, comme antarctique, *Euphausia superba*, l'émission des œufs est saisonnière et a lieu lors de pontes multiples. Nos estimations de fécondité sont basées sur le comptage des ovocytes mûrs formant un lot d'œufs dans les ovaires des femelles d'échantillons formolés. L'analyse en composantes principales et l'allométrie sont utilisées pour étudier la covariation de la taille d'un lot d'œufs avec d'autres charactères de la femelle. Chez les deux espèces, la taille du lot est proportionnelle au poids de l'ovaire, mais montre une allométrie majorante avec la longueur du corps. La taille moyenne d'un lot prédite à partir des relations d'allométrie est comprise entre 200 et 4 000 œufs pour *M. norvegica* mesurant de 25,5 à 35 mm et entre 1 500 et 6 000 œufs pour *E. superba* mesurant de 36 à 55 mm. Les relations d'allométrie peuvent être utilisées pour prédire la fecondité annuelle à partir de la structure de taille d'une population et en estimant le nombre de cycles de ponte par saison de reproduction. A cause de l'effet de la température sur la durée des cycles de mue et de ponte, on peut en inférer le nombre en prenant en compte le climat et ses variation saisonnières.

Introduction

Krill species play an important role in the pelagic ecosystem. Northern krill, *Meganyctiphanes norvegica*, and Antarctic krill, *Euphausia superba*, occur in large accumulations, providing food for large marine invertebrates (squids) and vertebrates from fish to fin whales. Both species reproduce during a limited period of the year and share a similar pattern of ovarian development, as illustrated in previous studies of the structure and development of the gonads in northern krill (Cuzin-Roudy 1993) and Antarctic krill (Cuzin-Roudy 1987).

Fecundity is difficult to estimate in euphausiids that release their eggs directly in the water column in multiple spawns, as described for *E. superba* (Ross and Quetin 1983; Nicol 1989), *M. norvegica* (Cuzin-Roudy and Buchholz 1999), *Euphausia pacifica* (Ross et al. 1982), and the subtropical species *Euphausia lucens* (Stuart 1992). The question of brood size is still being debated as well as the periodicity of the multiple spawns.

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During the reproductive season, all adult female krill are engaged in the development of a brood, but eggs are produced periodically and released in several spawning events. As the development of a new batch of eggs after a complete spawn has not yet been observed in the laboratory (Harrington and Ikeda 1986; Nicol et al. 1995; Cuzin-Roudy and Buchholz 1999), the potential for krill to release several broods during the reproductive season has been determined indirectly using the proportions of spawning females in large field samples maintained in the laboratory (Ross and Quetin 1983) or by staging the ovarian development (Cuzin-Roudy and Amsler 1991) in females from random samples taken at various times of the season (Cuzin-Roudy and Labat 1992; Labat and Cuzin-Roudy 1996; Cuzin-Roudy and Buchholz 1999).

The size of a brood has been obtained by direct counts of eggs released by krill spawning in captivity (for a review, see Ross and Quetin 1983), by counts of the developing oocytes in the ovary of preserved krill, or calculated from the volume of the ovary before and after spawning (for a review, see Mauchline and Fisher 1969). The number of eggs spawned has been related to the body size of krill (Ross and Quetin 1983; Nicol 1989; Nicol et al. 1995), but the relationship was weak and not predictive.

In both *M. norvegica* and *E. superba*, the ovary of reproducing females shows a similar structure. The brood is com-

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plex, with up to four groups of oocytes at different stages of development (Cuzin-Roudy 1987, 1993). Young oocytes and oocytes accumulating glycoproteic yolk (previtellogenesis) are present in the ovary throughout the reproductive season. Oocytes in the phase of lipid yolk accumulation (vitellogenesis) or already maturing (in meiosis) and mature form the next egg batch to be released and are easily distinguished from the rest of the brood in preserved krill. After spawning of the mature egg batch, the ovary is not empty, as recognized in previous studies (Mauchline and Fisher 1969; Makarov 1983). The most advanced previtellogenic oocytes have already started vitellogenesis for the preparation of a new egg batch. Vitellogenesis is a cyclical process linked to the molt cycle, as shown for *M. norvegica* (Cuzin-Roudy and Buchholz 1999), while previtellogenesis is permanent. Such a biphasic development for the brood proceeds throughout the whole reproductive season, resulting in a periodic production of egg batches.

In both krill species, spawning does not occur close to the actual molt (ecdysis). Laboratory-maintained *E. superba* in prespawning condition released one or up to three spawns apparently independent of the molt (Nicol 1989). According to Cuzin-Roudy and Buchholz (1999), *M. norvegica* spawn in coincidence with apolysis, when the epidermis resumes its activity for the preparation of the next molt. One to three spawns are released at molt stages D0 and D1. The distribution in random field samples of females at the various molt stages and sexual development stages (SDS) has shown that two successive molt cycles were necessary for a complete cycle of egg production, a "vitellogenic molt cycle" preceding the "spawning molt cycle."

The duration of the molt cycle (intermolt period (IMP)) is temperature dependent in *M. norvegica* (Cuzin-Roudy and Buchholz 1999) and varies with temperature in *E. superba* (Nicol and Stolp 1990). Fecundity of *E. superba* is known to fluctuate with year-to-year variation in the duration of the reproductive period, depending on the extent of ice cover (Spiridonov 1995) and food availability (Quetin and Ross 1991). Consequently, a summer increase in temperature should also result in an acceleration of spawning activity together with molting activity in *E. superba*.

We propose in the present study to limit the variability of fecundity data by counting separately the mature oocytes forming an egg batch in the ovary according to Cuzin-Roudy and Amsler (1991). Assuming that a field sample represents the state of sexual development of a krill population at the time of sampling, egg-batch size variation will be studied in relation to simultaneously recorded female characteristics. If female krill characteristics known to have different patterns and time scales of development, such as body size and weight, ovary weight, and egg-batch size, share major trends of covariation due to growth, allometric relationships can then be used in a predictive way at the population level for estimating egg-batch size from one or the other female characteristics and its distribution in the krill population.

Fecundity is defined here as the total number of eggs produced per female per year and is expressed as the number of eggs per batch per female multiplied by the number of possible reproductive cycles within the reproductive season. This number will be inferred from the information available concerning the duration of the season and the impact of temperature on molt and reproductive cycles. The final goal is to establish realistic estimates that could be the basis for numerical models predicting krill fecundity at the population level in various environments and climatic regimes.

Materials and methods

Krill samples

Meganyctiphanes norvegica samples were obtained during previous surveys: a multiyear survey of the Ligurian population, northwest Mediterranean Sea (Labat and Cuzin-Roudy 1996), and during cruises in the reproductive season in the Ligurian Sea (April 1996), the Kattegat, East Denmark (July 1996 and March 1997), and the Clyde Sea, West Scotland (June 1996), as detailed in Cuzin-Roudy and Buchholz (1999). Live female krill from field samples were maintained onboard for egg counts at spawning during the same cruises.

Euphausia superba samples were obtained from former surveys at three different locations and dates. Sample 1 was taken on a north–south transect south of the Scotia–Weddell confluence on December 20, 1988 (Cuzin-Roudy and Labat 1992). Sample 2, taken on January 24, 1992, in Admiralty Bay (King George Island), was part of a study of krill physiology by Buchholz et al. (1996). Two samples from the same area of the Prydz Bay region (Cuzin-Roudy 1987), taken on January 29 and February 4, 1985, were pooled into sample 3.

All samples were initially fixed in 10% buffered formalin and later preserved in 70% ethanol with 1% glycerol for better preservation of the cuticle. Such a treatment affords good fixation and preservation of the ovarian tissues. If wet weight is reduced by the treatment compared with fresh body weight, length–weight relationships are not changed (Kulka and Corey 1982).

Oocyte counts

Females from preserved field samples were measured individually for total body length (BL) from the tip of the rostrum to the end of uropods. The age-classes of *E. superba* were determined according to Siegel (1987) and Hosie et al. (1988), and for *M. norvegica* as in Labat and Cuzin-Roudy (1996).

Females were scored for SDS (Cuzin-Roudy and Amsler 1991; Cuzin-Roudy and Buchholz 1999). A sexual development index (SDI) (Cuzin-Roudy and Labat 1992) was established for each sample to express the average degree of sexual development of the population at the time and place of the sampling. The samples with similar SDIs were then pooled.

Total wet weight (WWT) and ovary wet weight (WWO) after complete dissection were recorded for each individual female. An ovarian lobe representing 15–25% of the total was weighed separately and then squashed, as described by Cuzin-Roudy and Amsler (1991) for *E. superba*, in order to separate and count the oocytes in each category as previtellogenic (PO: oc1 and oc2), vitellogenic (oc3), or mature oocytes (MO: late oc3 and mature oc4). The total number of mature oocytes (NMO) in the ovary was calculated for each female from the weight proportion of the part versus the entire ovary. Because of the centripetal development of the oocytes in the ovary, from the peripheral germinal zones to the center of each lobe, the part of ovary counted had to be a complete lobe in order to be representative of the entire ovary. NMO was taken as a measure of the size of the entire egg batch that will be released by the female before the next molt.

A total of 277 "ready to spawn" female *M. norvegica* (SDS 4 and SDS 5[1]) were individually dissected and scored for NMO and 76 were also scored for the number of previtellogenic oocytes (NPO). *Euphausia superba* females ($N = 82$) were scored for SDS, NMO, and NPO.

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Statistical analysis

Multivariate methods have been extensively used to identify patterns in ecological data sets (Gower 1987), and the theory of allometry has regained attention as a tool for studying the size dependence of biological characters, physiological rates, or productivity at the population level (Cyr and Pace 1993). Principal components analysis (PCA) is useful in the study of the covariation of quantitative morphometric descriptors. In the present study, rather than assuming a priori that egg-batch size should be correlated to female body size, PCA of the correlation matrix between the four log-transformed variables BL, WWT, WWO, and NMO was used to extract the main factors responsible for their common variation using the extensive data set obtained for *M. norvegica*. If the first principal component takes into account the largest part of the common variability, component 1 can be interpreted as a general size and growth factor. PCA of the matrix of covariance can then be used as the multivariate generalization of allometry (Jolicoeur 1963; Cuzin-Roudy and Laval 1975). The allometry coefficients (b PCA) are simply calculated two by two for the four variables from the ratios of their coefficients on vector 1 and compared with allometry coefficients obtained with bivariate allometry.

Allometric relationships were established using the allometric power function (for a review, see McArdle 1988)

$$(1) \qquad y = ax^b$$

and the coefficient of allometry b was calculated as the slope of the linear regression line for log–log-transformed data as

$$(2) \qquad \log y = a + b \log x$$

using regression models 1 and 2 (Sokal and Rohlf 1981). Model 1, the ordinary least squares (OLS) linear regression, is theoretically not adequate but is commonly used. Model 2, or "reduced major axis," has been devised for morphometric studies and better expresses the functional relationship of the two covarying variables (McArdle 1988). Logarithmic transformation of the data improves the normality of the distributions and the homogeneity of variance, both conditions required by the models. The allometry coefficient b was estimated with both models for a comparison, together with the Pearson coefficient of correlation (R) and determination (R^2) and analysis of variance F ratio for the OLS regression. The computations were done with SYSTAT for Windows 6.0.

Results

Northern krill populations

Characteristics of female M. norvegica

All adult females from the three samples had developing ovaries. They were in vitellogenesis (SDS 3), mature (SDS 4), spawning (SDS 5[1]), or had recently spawned (SDS 5[2]) and the average SDI was 4. The Clyde females were larger on average than the Ligurian or Kattegat krill, but NMO did not differ among the three samples. The 95% confidence intervals (CI) for NMO were 1064–1324 for the Kattegat sample, 898–1131 for the Ligurian sample, and 1065–1378 for the Clyde sample. The three samples were pooled for the analysis of brood size and body size and weight characteristics. In the pooled sample (N = 277), the range of body size was large (Table 1), from young females (0+) spawning for the first time early in the season to large females (2+) in their second spawning season. The weight of the ovary averaged 8% of the total body weight.

Table 1. Size and weight characteristics and number of eggs per batch in the ovary of the mature female *M. norvegica* of the pooled sample from the three populations.

Characteristic	N	Range	Mean	SE
BL (mm)	277	22.5–40.2	30.8	0.20
WWT (mg)	258	76–507	223	5.10
WWO (mg)	274	2–62	18	0.67
NMO	277	176–5320	1147	41.4

Variance analysis

After logarithmic transformation, G1 and G2 for skewness and kurtosis became non-significant ($P > 0.05$) for the four variables, and their overall distribution could be considered as multinormal. The first three components of the PCA of the correlation matrix (Table 2) of the four log-transformed variables explained 99% of the total variance, with 75% for the first component. Body size and weight, and to a lesser degree ovary weight and NMO, had high positive loadings for component 1. Component 2 (16%) was characteristic of the size of the egg batch and component 3 (8%) of ovary weight.

Component 1, the principal axis of the multivariate cloud of data for the four variables, expresses the general common trend of variation due to the size and weight increase of all body parts and organs with general growth. It can be interpreted as a general "growth factor." Factor 2 represented an "egg-batch factor" and factor 3 an "ovarian factor". The fact that factor 2 explained a larger part of the total variance than factor 3 emphasized the predominant role played by the periodic vitellogenic phase in egg-batch growth, at least partly independent from overall growth of the ovary and the entire brood.

Egg-batch size

The size of an egg batch estimated by counting the mature and maturing oocytes in ovaries of ready to spawn female krill (SDS 4 and SDS 5[1]) was around 1000–1200 eggs·batch^{-1} for a female of mean size and weight (Table 1). NPO, also counted for the Ligurian population, ranged from 110 to 10 699, with a mean of 2133 ± 416 previtellogenic oocytes·female^{-1} (95% CI). Moreover, numerous (not counted) young oocytes were present in the peripheral germinal zones. This indicated a potential for female krill to develop a minimum of two more egg batches after the release of the mature one.

Allometric relationships were established between the size of an egg batch (NMO) and BL, WWT, and WWO for the female krill from the pooled sample (Table 3). Significant correlation and regressions were obtained with OLS regression, but only 22% of the variance of the size of a batch was accounted for by the OLS regression with BL and 32% with WWO. A better fit to the data was obtained with the reduced major axis (RMA) regression model, as shown for the bivariate data cloud of NMO with BL (Fig. 1). The value of the allometric coefficient b RMA differed from b OLS when the correlation R was lower than 1. With b RMA, the relationships WWT/BL and NMO/WWO were not different from isometry; WWO/BL, WWO/WWT, NMO/BL, NMO/WWT scaled allometrically, with the ovary of mature

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Table 2. Correlation matrix of the four log-transformed variables BL, WWT, WWO, and NMO for female *M. norvegica* of the pooled sample (N = 277). PCA = principal component analysis.

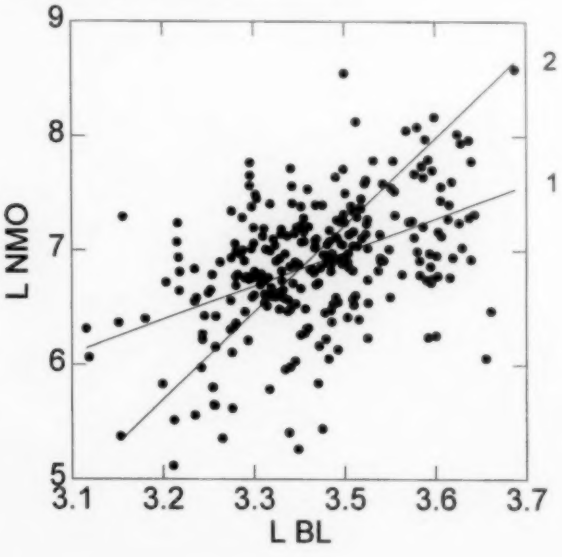
Variable	L BL	L WWT	L WWO	L NMO
L BL	1	0.943	0.713	0.475
L WWT		1	0.709	0.465
L WWO			1	0.550
L NMO				1
PCA (% variance)				
Component 1	Component 2	Component 3	Component 4	
75	16	8	1	
Component 1 loading				
L BL	L WWT	L WWO	L NMO	
0.926	0.930	0.861	0.689	

Table 3. Allometric relationship ($y = ax^b$) BL, WWT, WWO, and NMO for the ready to spawn female *M. norvegica* of the pooled sample.

Allometric relationship y/x	N	b OLS	b SE	R^2	ANOVA F ratio	b RMA	b PCA	Predicted NMO
WWT/BL	258	3.1	0.07	0.888	2036.71***	3.4	2.8	
WWO/BL	274	4.0	0.24	0.509	281.84***	5.6	6.8	
WWO/WWT	258	1.2	0.09	0.502	183.21***	1.7	1.9	
NMO/BL	277	2.5	0.28	0.219	80.22***	5.2	5.6	199–4069
NMO/WWT	258	0.7	0.09	0.209	70.56 ***	1.6	1.6	197–4083
NMO/WWO	273	0.5	0.05	0.325	130.28***	0.9	0.8	168–3514

Note: N, number of mature females; b, coefficient of allometry obtained with OLS regression (model 1), with RMA (model 2), and from the first vector of PCA of the covariance matrix of log-transformed data; b SE, standard error of b OLS and b RMA. The R^2 and ANOVA F ratios are given for the OLS linear regressions. NMO per batch is predicted from the RMA regressions for the smallest and the largest BL observed. Significance: ***$P < 0.001$.

Fig. 1. Logarithmic plot of NMO (L NMO) versus BL (L BL) for reproducing female *M. norvegica* (N = 112). A better fit is obtained with the model 2 (RMA) linear regression (2) than with model 1 (OLS) (1), allowing egg-batch size prediction from krill BL. Egg-batch size scales allometrically with BL (b RMA = 5.2), indicating a faster rate of increase.



females and egg-batch size increasing at higher rate than overall body size ($b > 3$) and weight ($b > 1$).

The values of the allometric coefficients obtained from the general allometry with component 1 of the PCA (b PCA, Table 3) were different from OLS but equivalent to b RMA. The validity of the RMA model for the description of the relationships of the size of a brood with other female krill size and weight characteristics was confirmed.

Consequently, the size of an egg batch (NMO) was predicted using RMA (model 2) linear regression on log-transformed data with body size and ovarian weight. Because the standard error of b is smaller for the relationship with ovarian weight, WWO can be preferred as the characteristic of reference, but BL is measured routinely on krill samples. The predicted egg-batch sizes for the smallest and the largest ready to spawn female krill observed in the pooled sample are given in Table 3. Compared with the observed range (176–5320 mature oocytes), these predicted egg-batch sizes were slightly underestimated for NMO/WWO with b = 0.9 instead of 1. But, as a mature egg batch occupies only part of the volume of the developing ovary, a slightly lower coefficient of proportionality is realistic.

Antarctic krill populations

Characteristics of female E. superba

All the female krill had developing ovaries, but, at difference with the northern krill samples, females from the three

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locations and dates of sampling differed in their stage of sexual development. Most females of the December (Scotia–Weddell) sample had previtellogenic ovaries (SDS 3 and SDS 4) or vitellogenic ovaries (SDS 5 and SDS 6). Some females had a small number of residual mature oocytes in the center of the ovarian lobes, indicating that they had already developed and released an egg batch (SDS 8). The average SDI was 6. Such an ovarian development was typical of an early summer situation.

The January (Admiralty Bay) sample was typical of the full reproductive season, as all females were vitellogenic (SDS 5 and SDS 6), ready to spawn (SDS 7), or recently postspawn (SDS 8), with SDI = 7.

The February samples (Prydz Bay region) showed an ovarian structure almost the reverse of the December sample (Scotia–Weddell). Most females (81%) were SDS 7 with predominant late vitellogenic and mature oocytes. The others were SDS 8, with few previtellogenic and young oocytes and even SDS 9, indicating the end of egg production for the season.

In the pooled sample, the BL range was large (Table 4) and age groups 2+ up to 5+ were represented. Prydz Bay females were larger in comparison with the others, and the continuity of adult size necessary for the study of the relationships between egg-batch size (NMO) and female size and weight characteristics (BL, WWT, and WWO) was represented in the sample (Table 4). The range of the different measurements showed that when the body size of a growing female krill was multiplied by 1.5 and body weight by 5; the ovarian weight was multiplied by 100.

About half of the females of the pooled sample were vitellogenic and spawning (SDS 5, SDS 6, and SDS 7), and egg-batch size could be estimated for 42 females only. Previtellogenic oocytes were also counted when present in the brood and for females at SDS 3 and SDS 4. Other krill were recently postspawn (SDS 8) and few were spent (SDS 9). The average state of development of the pooled sample was SDI = 7. A zero value for a category of oocyte in an individual krill is informative concerning the stage of development of the ovary but misleading when calculating average oocytes numbers. Zero values have been excluded for the calculation of the means in Table 4.

Egg-batch size

The variance analysis with PCA was not repeated for *E. superba* because of the small number of mature females in the sample, which did not allow a meaningful comparison with the *M. norvegica* sample. Based on the fact that all stages of the krill ovarian development were represented in the *E. superba* sample, as well as a large size range, we assumed that the pattern of covariation of female characteristics was not different for the two krill species. Allometric relationships were established in the same way as for *M. norvegica* using OLS and RMA for log-transformed data (Table 5). The OLS linear regressions were all significant, but the best fit was obtained with the RMA model. The part of the variability explained by the regression was the highest for WWT/BL (88%), with 75% for WWO/WWT and 63% for WWO/BL. With b RMA, isometry was found for WWO/WWT, with a slight positive allometric scaling for WWT/BL and a pronounced one for WWO/BL. WWO increases at a much higher rate than BL (95% CI for b RMA = 9.9–13.8), and large females produce relatively much larger egg batches than small females.

Table 4. Characteristics of female *E. superba* from the pooled sample.

Characteristic	*N*	Range	Mean	SE
BL (mm)	82	36.2–54.8	44.97	0.057
WWT (mg)	82	334–1645	820	40
WWO (mg)	82	5–550	132	17
NPO	76	0–10 690	2912	285
NMO	76	0–8813	3779	258
NOCT	76	9–10 690	3806	277

Note: Zero values were omitted for the calculation of mean numbers of oocytes when one category was absent.

Considering the relationship of the number of oocytes with the size and weight characteristics (Table 5), the total number of developing oocytes (oc1, oc2, oc3, and oc4) (NOCT) was proportional to the weight of the ovary (isometry for NOCT/WWO). Interestingly, the relationship of previtellogenic oocytes to ovarian weight (NPO/WWO) scaled with a negative allometry (b = –1.2), reflecting a tendency for large females to have a smaller stock of previtellogenic oocytes than small females. The regression of the egg-batch size with ovary weight (NMO/WWO) was significant, with 84% of the variance of NMO explained by the ovarian weight, but Fig. 2 shows that a better fit to the scatter of points was obtained with two regression lines, one for krill with small ovaries (1 in Table 5) and the other for krill with large ovaries (2 in Table 5). The change of slope between the two lines corresponded to an ovarian weight of 70 mg. The first line described the relationship for females with small or partially spawned ovaries. From the relationship WWO/BL, an ovarian weight of 70 mg corresponded to a BL of 45 mm and to the age group 3+. Small females from age group 2+, which were in their first reproductive season, did not follow the same pattern of egg-batch growth as large females.

Correlation was high (R = 0.835) for the second line, and scaling for egg-batch size with ovary weight (NMO/WWO) was isometric for females of different sizes from age groups 3+, 4+, and 5+. Relationship 2 was chosen to predict the size of an egg batch for ready to spawn females of different sizes and age-classes. With b RMA = 0.9, the mean number of eggs in a batch was 3304 eggs, from 1534 to 6022 eggs for the range of ovarian weight observed in the pooled sample (Table 5).

From the relationships WWO/BL, (1) NMO/WWO, and (2) NMO/WWO (Table 5), we can predict the egg-batch size for the central size-class of the different age groups, as presented in Table 6. Large 5+ krill would have 35 times more eggs in a batch than young 2+ krill.

Discussion

Seasonal pattern of ovarian development in *E. superba*

Despite the different locations of the sampling, the individual variability of ovarian structure observed among female *E. superba* illustrated a seasonal pattern for ovarian development, if each individual structure is viewed as representing one step of the development of the brood.

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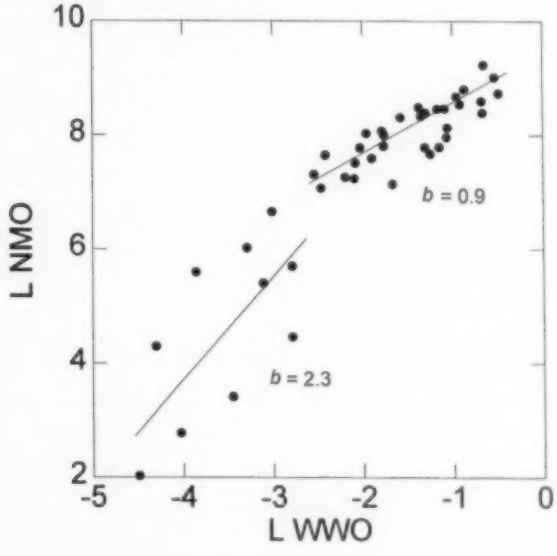
Table 5. Allometric relationships between BL, WWT, WWO, and oocyte numbers in reproducing female *E. superba*.

Allometric relationship *y*/*x*	*N*	*b* OLS	*b* SE	R^2	ANOVA *F* ratio	*b* RMA	Predicted NMO
WWT/BL	82	3.5	0.18	0.884	606.98***	3.7	
WWO/BL	82	9.1	0.79	0.625	133.21***	11.5	
WWO/WWT	82	2.7	0.17	0.749	239.11***	3.1	
NOCT/WWO	76	0.4	0.10	0.168	14.95***	0.9	
NPO/WWO	57	–0.4	0.15	0.098	5.98*	–1.2	111 – 34 889
NMO/WWO	42	1.5	0.10	0.836	204.59***	1.6	23 – 12 654
(1) NMO/WWO	10	1.7	0.59	0.500	7.99*	2.3	
(2) NMO/WWO	32	0.8	0.09	0.697	69.02***	0.9	1 534–6 022

Note: The R^2 and ANOVA *F* ratio are given for the log–log OLS linear regressions. The coefficient of allometry is estimated as the coefficient of regression *b* from $\log y = a + b \log x$ using OLS and RMA regression models. Significance: $*P < 0.05$; $***P < 0.001$.

Fig. 2. Logarithmic plot of NMO (L NMO) versus WWO (L WWO) for a sample ($N = 42$) of ready to spawn female *E. superba*. A better fit was obtained with two regression lines (model 2, RMA), separating large females from small ones. Egg-batch size is proportional (isometric) to ovary weight and can be more accurately predicted for females with ovary weight over 70 mg and BL over 45 mm.



Based also on data from previous studies (Cuzin-Roudy and Amsler 1991; Cuzin-Roudy 1993), a synthetic model is proposed (Fig. 3) to describe the seasonal reproductive development of *E. superba*. Reproduction is limited to the short summer, with year-to-year variations (Quetin and Ross 1991). In late spring, adult females of various sizes (i.e., from age-classes 2+, 3+, and older) start to accumulate glycoproteic yolk (previtellogenesis) in young oocytes previously produced in large numbers by the activity of the oogonia (SDS 2 or SDS 10). The majority of the females then become SDS 3 and SDS 4, as illustrated in the present study by the December sample. Previtellogenesis will go on continuously until the end of the reproductive period. Periodically, when the most advanced previtellogenic oocytes have attained a certain size, they form a batch and enter a cycle of lipid yolk accumulation (vitellogenesis) (SDS 5 and SDS 6), maturation through meiosis (SDS 7), and release in one to three spawning events (not detailed in Fig. 3). The postspawn ovary (SDS 8) still contains numerous oocytes ready for the next cycle of vitellogenesis, maturation, and spawning (SDS 4). The January sample illustrated such a full reproductive activity. The cyclical development of egg batches stops when previtellogenesis is arrested and all the unreleased oocytes from the developing brood undergo oosorption (SDS 9), as illustrated for some females of the February sample. At this time, oogonia activity is still high and the ovary is rapidly reorganized and filled again with young oocytes (SDS 10), which will not develop further during the long sexual rest. Females from the samples studied here illustrated all the successive SDSs followed by reproducing female krill, from SDS 3 to SDS 9.

Table 6. Predicted size of a *E. superba* egg batch (egg number) for the central size-class of age groups calculated from the RMA regressions fitted as in Fig. 2.

Age group (years)	Size-class (mm)	Mean ovarian weight (mg)	Mean predicted egg number
2+	39–40	13	230
3+	44–45	59	929
4+	50–51	254	3558
5+	54–55	607	7932

Compared with the pattern defined for *M. norvegica* (Cuzin-Roudy and Buchholz 1999), 10 SDSs were necessary to describe *E. superba* development, which is more extended in time. For example, 1 month is necessary for Ligurian Sea *M. norvegica* to complete previtellogenesis and the first vitellogenic cycle (SDS 2 to SDS 5) for spawning in February, while some *E. superba* females were observed at SDS 3 (previtellogenesis, Fig. 3) from November to early January, when others were already mature and spawning (Cuzin-Roudy and Labat 1992).

Egg-batch size

As reviewed by Mauchline and Fisher (1969), fecundity of *M. norvegica* was estimated as 350–500 eggs for the Clyde Sea population and 500 eggs on average for the Ligurian Sea population, assuming only one brood per sea-

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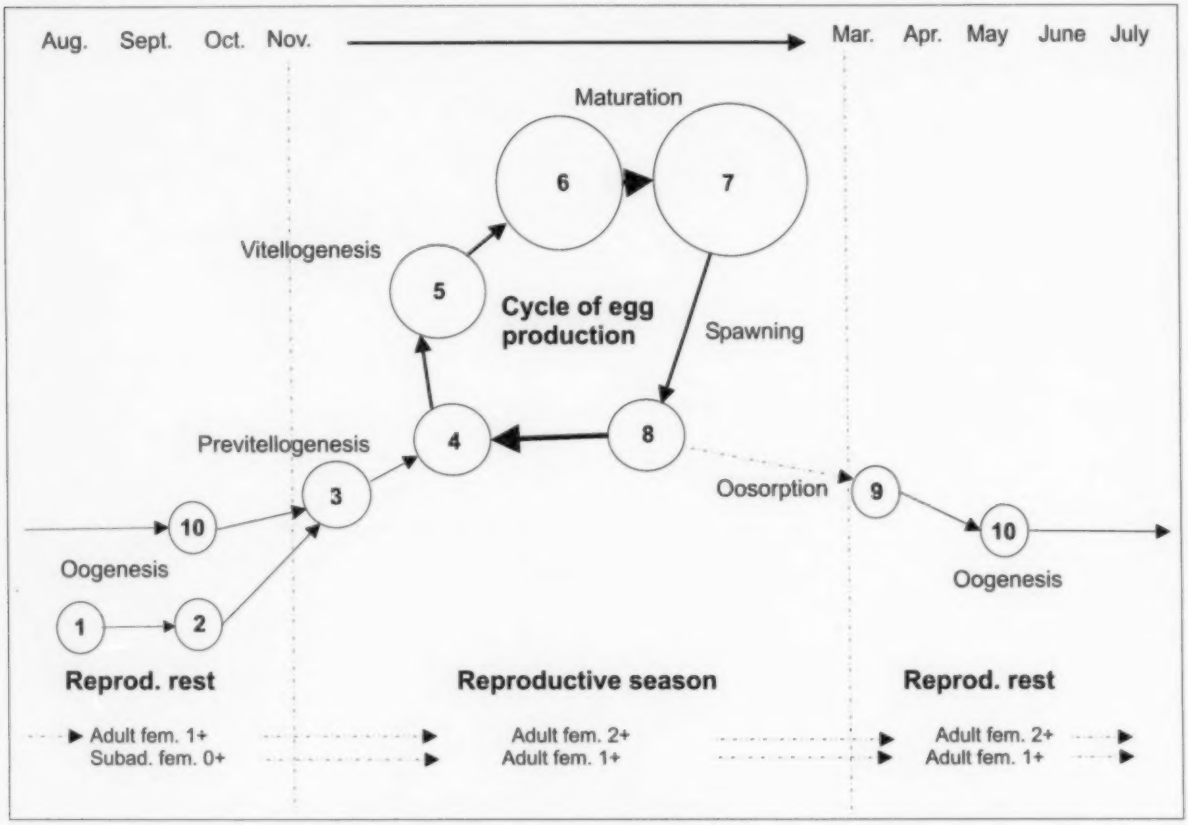
Fig. 3. Seasonal pattern of ovarian development in *E. superba*. The succession of SDSs illustrates the alternation of a summer reproductive period and a winter rest for adult female krill from age groups 2+, 3+ etc. The onset of the reproductive season is marked by previtellogenesis (SDS 3 and SDS 4) for adult female krill of all sizes and ages. Later on, successive cycles of vitellogenesis and maturation produce successive egg batches. The end of egg production is due to an arrest of oocyte development and to oosorption. The ovary regains a juvenile structure (SDS 9 and SDS 10) during the reproductive rest. The onset and duration of the reproductive season may vary from year to year as well as the number of successive cycles of egg production during one season.



son for individual female krill and an undetermined life span.

As a partial spawn can be of any size, from a complete egg batch to a few residual eggs, the number of eggs released by krill at one spawning event is expected to underestimate the actual size of the egg batch and cannot be taken as an estimate of fecundity. Adding the partial spawns observed before the molt that ends the spawning molt cycle should reduce the bias. Counts of eggs released during the premolt period by *M. norvegica* in Cuzin-Roudy and Buchholz (1999) yielded mean estimates that did not differ among the three populations studied. The largest spawn released by an individual krill was 900 eggs for the Ligurian sample and 1500 eggs for the Clyde krill, which also attained a larger average body size. Despite the differences in spawning rhythm, the total number of eggs released per female krill during the premolt period of a spawning molt cycle, obtained by adding the partial spawns, was not significantly different for the three populations: 650 ± 130 eggs·female^{-1}. These estimates were consistent with numbers given in the literature, about 500 eggs·female^{-1} (see Mauchline and Fisher 1969), but were largely underestimated compared with the average egg-batch size of 1000 eggs estimated from oocyte counts.

According to previous investigations (for reviews, see Harrington and Ikeda 1986; Nicol 1989), estimates for *E. superba* fecundity vary from 310–800 eggs released in one spawning event (Mauchline and Fisher 1969) to 2500 eggs·spawn^{-1} and up to nine spawning episodes in one season (Ross and Quetin 1983). With the recognition of partial spawning also in *E. superba* (Makarov 1983) and a better knowledge of the pattern of ovarian development, ready to spawn females can be distinguished from partially spawned ones. Then, more accurate estimates for egg-batch size can also be obtained for *E. superba* from counts of mature oocytes in krill with fully developed ovaries.

In this study, the large sample of *M. norvegica* females allowed an analysis of the total variance of egg-batch size together with female size, weight, and ovary weight using PCA and multivariate allometry (Jolicoeur 1963). If ovarian weight and egg-batch size showed specific trends of variability, they nevertheless largely varied with overall body size

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and weight. The comparison of the multivariate model (PCA) with bivariate models of regression analysis (OLS and RMA) showed that RMA was the best predictive model, as it gave results equivalent to those of PCA but is much easier to compute. In *M. norvegica*, egg-batch size was directly proportional to ovary weight, but the ovary was growing at a much higher rate than female size, reflecting the periodic development of egg batches. Moreover, the size of an egg batch clearly scaled allometrically with the size of the female, allowing the prediction of egg-batch size from female BL. Within the size range represented in the krill sample, the egg number in a batch was multiplied by 20 when BL doubled.

From the literature, a female *E. superba* of 40 mm mean BL released 1340 eggs on average (Ross and Quetin 1983); a female of 50.22 mm mean BL released 1914 eggs (Nicol et al. 1995). The egg numbers predicted here from the relationships with body size and weight and ovarian weight were higher but were not in contradiction with the numbers obtained from ovarian counts by Siegel (1985): 500–5000 eggs for krill of 40–60 mm BL. Due to a higher rate of growth, egg-batch size was multiplied by 30 when body size was multiplied by 1.5.

With similar allometric scaling in both krill species for the size of a batch versus ovary weight, larger egg batches are produced by *E. superba* because of a much larger body size attained during a long life cycle. This is in agreement with the conspicuous "overswollen" ovary of large ready to spawn females. Small krill, more abundant in the spring sample, had smaller egg batches and most of them were also less advanced in ovarian development than large krill, a trend already recognized in the literature (Siegel 1985; Cuzin-Roudy and Labat 1992). We take this as an indication that the biphasic pattern of ovarian development was not completely established for age group 2+ female *E. superba* reproducing for the first time.

Reproductive cycles and fecundity estimates

We know for *M. norvegica* that the timing for spawning is linked to premolt stages D0 and D1 (Cuzin-Roudy and Buchholz 1999). A similar trend was observed for *E. superba*, as spawning occurred during premolt stages D0 to D2 for females scored for molt stage at the time of spawning (Cuzin-Roudy 1987; Buchholz 1991; Buchholz et al. 1996). In the present study, all of the ready to spawn *E. superba* (SDS 7) were in molt stage C/D0, D1, or D2, and recently postspawn females (SDS 8) were in every molt stage (data not shown). These results are in agreement with the observation by Nicol (1989) of a sample of female Antarctic krill spawning in synchrony and producing one, two, or three spawns within 36 h of the initial spawning and 10.8 days on average before the actual molt (ecdysis). We take this as an indication that spawning is also linked to the premolt phase of spawning molt cycles in *E. superba*. Even if the precise links between spawning and molt preparation still have to be established for Antarctic krill, a complete cycle of egg production (vitellogenesis, maturation, and spawning) is likely to last more than one molt cycle, with alternate vitellogenic molt cycles for lipid yolk accumulation.

In the present study, previtellogenic oocytes were two times more numerous than mature ones in ovaries of *M. norvegica*, while previtellogenic and mature oocytes were in equivalent numbers in *E. superba* ovaries. This was taken as an indication that the previtellogenic oocytes form the next egg batch after the release of the mature one, with a potential of three successive batches for *M. norvegica* and two for *E. superba*.

The number of broods produced per year cannot be evaluated for a krill population without considering the effect of climatic and trophic conditions on the reproductive cycles. For *M. norvegica*, the effect of temperature changes on the duration of the molt cycle (IMP) has been established (Cuzin-Roudy and Buchholz 1999) and can be used to predict the periodicity of the spawning molt cycles. For three populations adapted to different temperature regimes (Clyde Sea, Kattegat and Ligurian Sea), IMP varied during the reproductive season from 6.5 to 16 days, corresponding to a temperature range of 14–4°C. Together with short IMPs, high molting and high spawning rates coincide with a short reproductive season in warm climates (Ligurian Sea population), while populations in colder areas (Kattegat, Clyde Sea) show longer IMPs together with a longer reproductive season; the number of spawning cycles, and consequently fecundity, should finally be similar for the three populations. Assuming that trophic conditions are not limiting when female krill produce eggs, a conservative estimate predicted by the large number of oocytes developing simultaneously through previtellogenesis and vitellogenesis in the ovary is a minimum of three successive egg batches. A maximum of six reproductive cycles (6 × 2 IMPs) can be deduced from the duration of the season at the three sites: 3 months for the Ligurian Sea, 5 months for the Clyde Sea, and 6 months for Kattegat on average from year-to-year variations (Cuzin-Roudy and Buchholz 1999). Then the range of annual egg production (at 1000 eggs·batch^{-1}) for a mean-sized individual female *M. norvegica* was estimated as approximately 3000 eggs·female^{-1}·year^{-1} to potentially 6000 eggs·female^{-1}· year^{-1}.

As a result of an acceleration of the molt cycles with increased temperatures, spawning frequency should be also higher for *E. superba* when temperature increases in summer. In euphausiid species adapted to high temperatures, such as the Ligurian *M. norvegica* (IMP = 7 days) or subtropical *E. lucens* (IMP = 4 days; Stuart 1992), multiple spawning and short reproductive periods for individual females will result in an apparent continuous egg production at the population level. In *E. superba*, IMP varies from 12.5 days at 4.5°C to 29.6 days at –0.5°C, with IMP = 25.3 days at 0°C (as reviewed in Nicol 1989). Finally, a more than twofold decrease in IMP results from an increase in temperature of 10°C for *M. norvegica* and 5°C for *E. superba*, i.e., in both cases for the range of temperature encountered in situ by krill

From the spawning frequency and the interval between spawning episodes of Antarctic krill sampled west of the South Shetland Islands, Ross and Quetin (1986) estimated seven spawning episodes on average per season. As IMP can vary from 29.6 to 12.5 days with temperature increase in summer, our estimate would be, for a reproductive season of 3 months, four IMPs for two reproductive cycles, with three partial spawns each, i.e., six spawning episodes. With the

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distinction between complete egg batches and partial spawns, *E. superba* fecundity, with 3779 eggs·batch^{-1} for an average-sized female, is estimated here as 7500 eggs·female^{-1}·year^{-1}.

The positive allometric scaling found for egg-batch size with body size in both krill species indicated that fecundity is a function of the size structure of the population and of krill growth rate. Krill populations with a high proportion of large females from the beginning of the reproductive season, as a result of high larval and juvenile growth rates or overwintering success of older females, should also achieve a high fecundity.

Due to a long life span lasting over 4 years (Ikeda 1985), *E. superba* attains a larger size than *M. norvegica* with a life span of 2–3 years (Mauchline and Fisher1969; Labat and Cuzin-Roudy 1996) and consequently produces larger egg batches.

But more studies are necessary to demonstrate differences in fecundity among different krill populations. Seasonal and year-to-year variations in the trophic conditions must be considered. They certainly determine growth rates and spawning frequency and may also influence the onset and duration of the reproductive season. It is well accepted that *E. superba* can grow and reproduce only in highly productive areas, with large year-to-year variations in the onset and duration of the reproductive season for different areas of the krill habitat (Ross and Quetin 1986; Spiridonov 1995). This is in agreement with field observations (Cuzin-Roudy 1993) and experimental results (Cuzin-Roudy 1987; Cuzin-Roudy and Buchholz 1999) concerning oosorption. In the case of poor feeding in laboratory conditions, the ovary of *M. norvegica* reacted very rapidly (in 2–4 days for the Ligurian and Kattegat populations, respectively) and shifted from yolk accumulation to oosorption.

In the present study, we chose to address the basic physiological patterns of krill reproductive cycles to estimate potential fecundity, making the assumption that krill could not produce high-energy-packed egg batches (Ross and Quetin 1986; Cuzin-Roudy et al. 1999) in an unfavorable trophic environment.

The pattern of yolk accumulation in two phases with a different time scale is an efficient strategy for coping with variations in the trophic regime. Glycoproteic yolk accumulation (previtellogenesis) is slow and progressive throughout the whole reproductive season, while lipid yolk accumulation (vitellogenesis) and final egg maturation occur in short cycles. Storage for reproduction involves, in both species, a well-developed fat body, which is always associated with the active ovary and may also buffer an eventual instability in resources. Specific differences appear concerning lipid metabolism. Both the ovary and fat body accumulate high triglycerides levels in reproductive *E. superba* females (Mayzaud et al. 1998), while polar lipids with high levels of polyunsaturated fatty acids are preferentially accumulated in *M. norvegica*. Triglycerides are accumulated in the digestive gland year-round (Cuzin-Roudy et al. 1999). The rate of lipid accumulation in the eggs is likely to be accelerated by temperature together with the other developmental processes of the molt cycle. In *M. norvegica*, the highest possible rate of egg production was an egg batch of 1000 eggs produced every 15 days during a reproductive season of 3 months for an average female of the Ligurian population living year-round at an in situ temperature of 13°C (Cuzin-Roudy and Buchholz 1999).

Finally, in both northern and Antarctic krill, the specificity of the reproductive strategies concerning fecundity appeared to rely on a different timing for the basic physiological processes involved in a biphasic egg development, in close relationship with the female development throughout the life cycle. The results presently available allow us to conclude that fecundity of a krill population can be viewed as a function of several biological factors besides the biomass, such as the size structure and dynamics of the population. The potential to produce numerous eggs is realized under the control of climatic factors and limited by trophic conditions.

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Krill: a possible model for investigating the effects of ocean currents on the genetic structure of a pelagic invertebrate

Lorenzo Zane and Tomaso Patarnello

Abstract: This paper reviews the information available on the population genetics and systematics of krill (Euphausiidae, Crustacea), integrating the published data with new data collected in our laboratory. Phylogenetic analysis of several Antarctic and sub-Antarctic *Euphausia* species indicates the importance of dispersal in determining the present-day geographic distribution. Dating speciation events suggest that the formation of the Antarctic Convergence, the oceanographic barrier isolating the Southern Ocean, may have played a role in separating the ancestral Antarctic and sub-Antarctic lineages. Intraspecific data show that the Antarctic krill (*Euphausia superba*) is characterized by weak genetic differentiation, whereas the northern krill (*Meganyctiphanes norvegica*) is more structured showing discrete genetic pools. This difference can be explained, at least partly, by the oceanographic conditions in the areas inhabited by the two species.

Résumé : Nous examinons ici l'information disponible sur la génétique des populations et la systématique du krill (Euphausiidae, Crustacea) en intégrant aux données publiées de nouvelles données recueillies dans notre laboratoire. L'analyse phylogénétique de plusieurs espèces antarctiques et subantarctiques d'*Euphausia* révèle le rôle important de la dispersion dans la configuration actuelle de leur distribution géographique. La datation des événements de spéciation fait ressortir que la formation de la convergence antarctique, barrière océanographique qui isole l'océan Austral, peut être intervenue en séparant les lignées ancestrales antarctiques et subantarctiques. Les données intraspécifiques montrent que le krill antarctique, *Euphausia superba*, se caractérise par une faible différenciation génétique, alors que le krill boréal, *Meganyctiphanes norvegica*, est plus structuré et présente un fonds génétique distinct. Une telle différence peut s'expliquer, au moins en partie, par les conditions océanographiques qui règnent dans les régions où vivent ces deux espèces.

[Traduit par la Rédaction]

Introduction

In the last 20 years, molecular genetic investigations of marine organisms largely changed the perception of marine biodiversity and significantly contributed to our understanding of the evolutionary mechanisms acting on natural populations (Palumbi 1992). These studies, mostly focused on fish because of their economic importance, have shown high levels of genetic differentiation at the population level in many species, even within small geographic areas (Bowen and Grant 1997; Graves 1998).

These studies also showed that the degree of genetic differentiation can be linked to life history features. For instance, anadromous fish tend to be genetically more structured than marine species. This is interpreted as the effect of the high habitat patchiness experienced by anadromous fish that very likely creates opportunities for isolation and genetic divergence between populations. On the other hand, the relatively low level of genetic differentiation usually observed in pelagic species might be explained by high between-habitat continuity, large effective population size, and passive dispersal of pelagic larvae (Carvalho and Hauser 1998). In fact, the pelagic style of life seems to play a key role in preventing genetic differentiation: species with high larval dispersal are genetically more homogeneous than species having poor dispersal capacity, and this holds true for many taxa ranging from molluscs to echinoderms to corals (Palumbi 1996). However, exceptions to this general trend place emphasis on the importance of other factors that may have a role in creating and maintaining population differentiation. These factors include behavioral mechanisms limiting dispersal, selective processes, complex oceanographic patterns, and historical barriers to gene flow (Palumbi 1994). The interplay between these factors is important in speciation processes, as revealed by molecular genetics studies carried out at different taxonomic levels (Avise 1994).

Phylogenetic analyses can also be used to date cladogenetic events by means of the "molecular clock" (Zuckerkand and Pauling 1965). This offers the opportunity to directly test the temporal link between speciation and geological or climatic changes, eventually identifying vicariant events. On the other hand, allopatric speciation is not the only speciation model because speciation can take place in sympatry by the

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Table 1. List of species used in the phylogenetic analysis with the GenBank accession No. for the partial sequences of the two genes studied given in parentheses.

Species	16S	ND1
Euphausia superba	Patarnello et al. 1996 (Z73805)	This study (AF281263)
Euphausia crystallorophias	Patarnello et al. 1996 (Z73806)	This study (AF281264)
Euphausia frigida	This study (AF281276)	This study (AF281262)
Euphausia vallentini	Patarnello et al. 1996 (Z73804)	This study (AF281261)
Euphausia longirostris	This study (AF281273)	This study (AF281265)
Euphausia similis	This study (AF281274)	This study (AF281266)
Euphausia krohni	This study (AF281275)	This study (AF281267)
Meganyctiphanes norvegica	Patarnello et al. 1996 (Z73803)	This study (AF281268)
Thysanoessa macrura	Patarnello et al. 1996 (Z73802)	This study (AF281270)
Nematoscelis megalops	This study (AF281272)	This study (AF281269)
Stylocheiron maximum	This study (AF281277)	This study (AF281271)

development of ecoethological differences, which can act as a strong evolutionary force (Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999). In such a case, there will be no link between the formation of particular lineages in the evolutionary history of a group and geological or climatic events.

Although we are well in the mature stage of the application of molecular genetics to marine organisms, relatively few studies have been carried out on pelagic or planktonic invertebrates (Bucklin 1995). Some of the existing studies have been focused on krill; thus, the aim of this paper is to update the information available on the genetics of this organism, combining the published data at the intraspecific and interspecific level and integrating them with some new results.

Evolutionary questions

The biological and ecological importance of krill species is well known (see other contributions in this issue), and their relevance will be reviewed here only from an evolutionary point of view.

At the large geographic scale, the first striking feature characterizing the geographic distribution of the 85 krill species belonging to the family Euphausiidae is the wide range occupied by many of them, with some species being present in different oceans. It is worth noting that several krill species show a broadly overlapping distribution despite their similar ecology and life history. In this context, one could ask whether their present-day distribution is, to some extent, the result of speciation processes.

The following points appear relevant for better understanding krill evolution. (*i*) Are the neighboring (or codistributed) species more phylogenetically related to one another than species with disjunct distributions? (*ii*) Would it be possible, by using a molecular clock, to identify geological and (or) paleoclimatic events that have played a role in krill evolution?

Molecular phylogenetics appear particularly suitable to address these questions, especially considering that species relationships within the euphausiid family are poorly known. Moreover, it is of great importance to test the degree of genetic structure at the intraspecific level and possibly to relate the genetic heterogeneity (if any) to the present-day oceanographic pattern in order to evaluate the role of marine currents in krill microevolution. In this paper, the case of the Antarctic krill (*Euphausia superba*) and the northern krill (*Meganyctiphanes norvegica*) will be considered.

Genetic comparison at the interspecific level: vicariance and dispersal

The hypothesis of allopatric speciation fostered by vicariance was proposed to explain the pattern of evolution for Antarctic species of the genus *Euphausia* (Patarnello et al. 1996). In that study, phylogenetic relationships between several euphausiids were reconstructed by sequencing part of the 16S rRNA mitochondrial gene. The species analyzed included the two most abundant Antarctic *Euphausia* species, namely *E. superba* and *E. crystallorophias*, and the sub-Antarctic one, *E. vallentini*. The phylogenetic tree unambiguously clustered together the two Antarctic species, with *E. vallentini* as their sister group. In order to date the split between the Antarctic and the sub-Antarctic clades, the crab molecular clock was used after the homogeneity of the substitution rate between crab and krill 16S rRNA was verified (Cunningham et al. 1992). This allowed us to estimate the separation time of *E. vallentini* from the two Antarctic *Euphausia* spp. to between 19.3 and 20.2 million years ago (MYA) (for details, see Patarnello et al. 1996). Such estimates appeared to be in good agreement with the time of formation of the Antarctic Convergence, independently estimated based on geological evidence (22–25 MYA). It was concluded that the Antarctic Convergence might have represented a hydrographic barrier that could have promoted the separation of the ancestral lineage from which the Antarctic clade of the genus *Euphausia* evolved (Patarnello et al. 1996). Consequently, their present-day distribution was interpreted as resulting from vicariance.

We have now sequenced the same region of the 16S rRNA in four additional species of the genus *Euphausia* from a wider geographic area, and we have included two additional genera in the phylogenetic analysis, namely *Stylocheiron maximum* and *Nematoscelis megalops*. In addition, sequence information for part of the subunit 1 of the NADH dehydrogenase mitochondrial gene (ND1) has been obtained for all the species listed in Table 1. Phylogenetic trees based on this new data set were generated by different methods (distance, maximum parsimony, and maximum likelihood, implemented in PAUP* (Swofford 1998)), and all produced an identical tree topology (Fig. 1).

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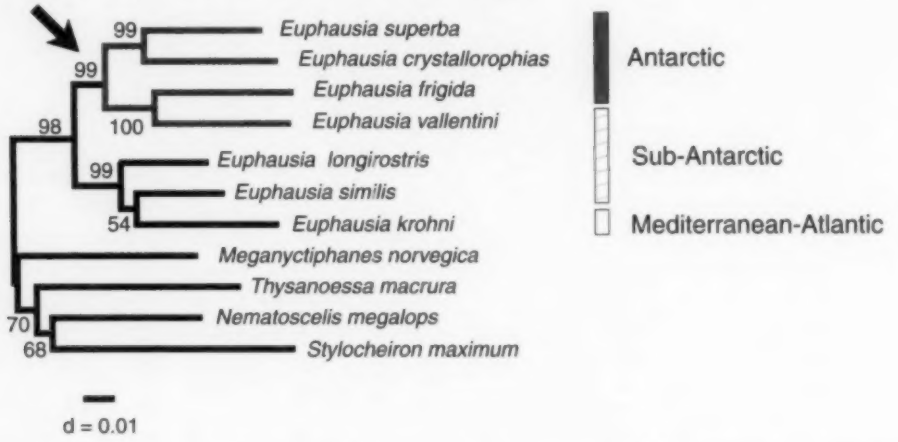
Fig. 1. Neighbour-joining tree (Saitou and Nei 1987) based on Kimura two-parameter distances (Kimura 1980). Identical topologies were generated using the maximum parsimony and maximum likelihood methods (trees not shown). Bootstrap values after 1000 replications are reported for well-supported nodes. The arrow indicates the split associated with the hypothesized vicariant event (see text). Bars on the left indicate the distribution of the *Euphausia* species analyzed. The tree is based on a combined data set of about 440 base pairs of the 16S rRNA gene and of 387 base pairs of the ND1 gene. The 16S rRNA sequence was obtained following previously published protocols (Patarnello et al. 1996). The ND1 sequence was obtained by PCR amplification of the entire gene with the two primers tRNAMn (5′-CAGAGGGATGCTCAGGATTTA-3′) and CbMnL3 (5′-CGGAGCTCGAACCTGTAGAAGA-3′) followed by cycle-sequencing with tRNAMn (L. Zane and T. Patarnello, unpublished data).



The phylogenetic reconstruction showed the genus *Euphausia* to be monophyletic with high bootstrap support, irrespective of the species (of the four non-*Euphausia* species) chosen to root the tree. In addition, when the *Euphausia* clade was forced to be paraphyletic, the resulting tree topologies were significantly worse than topologies supporting their monophyly ($P < 0.05$), as revealed by the Kishino–Hasegawa log-likelihood test (Kishino and Hasegawa 1989).

Inside the *Euphausia* clade, all nodes were supported by high bootstrap values. Within this clade, two distinct lineages emerged, one grouping together *E. krohni* (an *Euphausia* known to occur in the Mediterranean), *E. similis*, and *E. longirostris* (two sub-Antarctic species with distribution similar to *E. vallentini*) and a second clade including *E. superba*, *E. crystallorophias*, and *E. vallentini*, as in Patarnello et al. (1996), with the addition of *E. frigida*, a fully Antarctic species.

Interestingly, *E. frigida* was placed as a sister species of the sub-Antarctic *E. vallentini* and not in monophyly with the other Antarctic species *E. superba* and *E. crystallorophias*. This branching order is supported by the Kishino–Hasegawa log-likelihood test that significantly rejects any alternative tree constrained so as to include *E. frigida* in the "Antarctic" clade ($P < 0.05$).

We estimated the date of splits between species by applying the molecular clock following the previously published approach (Patarnello et al. 1996). For this purpose, only the 16S rRNA sequence data were used in order to apply the mutation rate already reported for this gene in crab (Cunningham et al. 1992). The enforcement of the molecular clock requires that mutations accumulate homogeneously between lineages and in a linear manner with respect to time; if this holds true, then it is possible to translate genetic divergence into time of divergence (Takezaki et al. 1995). In order to assess homogeneity of the mutation rate between the taxa investigated in this work, we applied the two-cluster test as described in Takezaki et al. (1995). The 11 species analyzed showed a homogeneous rate of transversions. This allowed us to use the 16S transversions to reconstruct a linearized tree, that is, a clock-constrained tree in which all the tips are forced to be contemporary. The linearized tree is based on genetic divergences corrected to fit the assumptions of molecular clock that are calculated by the ordinary least squares method (Takezaki et al. 1995). The values of the corrected genetic divergences can be used to date any node of the tree.

Applying the same molecular clock previously used for krill 16S rRNA, a rate for transversion of 0.155–0.170% per million years (Cunningham et al. 1992), and considering the corrected genetic distance between *E. vallentini* and *E. frigida* (0.0122, calculated on 16S rRNA transversions only), the split between these two species from the common ancestor is on the order of 7.9–7.2 MYA. The separation of *E. superba* from *E. crystallorophias*, with a corrected distance of 0.0048, is estimated to be on the order of 3.1–2.8 MYA.

When the same calculation is applied for estimating the split between the Antarctic clade (*E. superba* and *E. crystallorophias*) and the sister clade (*E. vallentini* and *E. frigida*), the genetic divergence of 0.0421 results in a separation of about 27.2–24.8 MYA. This value is slightly inflated when compared with the 20.2–19.3 MYA reported previously (Patarnello et al. 1996), due to the inclusion of *E. frigida* in the analysis. However, both results are still compatible with the period of formation of the Antarctic Convergence (25–22 MYA).

On the basis of these results and still assuming that the Antarctic clade originated by isolation, the present-day distribution of *E. frigida* (south to the Antarctic Convergence) could be interpreted as a dispersal event. The speciation pro-

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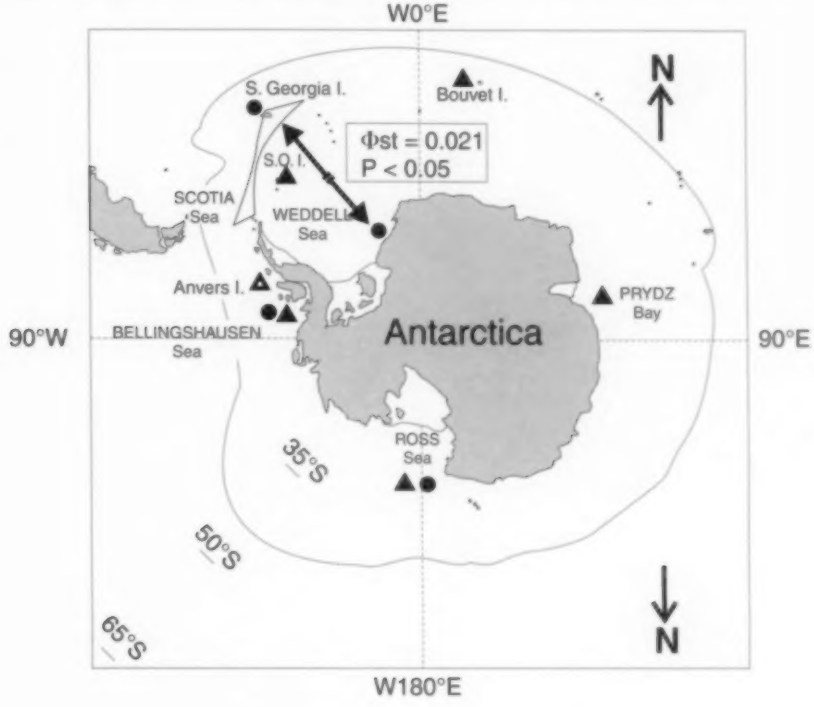
Fig. 2. *Euphausia superba* samples analyzed in previous investigations. Solid triangles indicate geographic areas studied with allozyme markers (from Fevolden and Schneppenheim 1989); the open triangle indicates the Anvers Island sample (Fevolden and Ayala 1981). Circles indicate samples analyzed by mtDNA sequencing (Zane et al. 1998). With regard to the latter study, significant Φ_{st} and the associated *P* value are reported together, with arrows indicating the two genetically heterogeneous samples. The shaded area indicates the Scotia–Weddell confluence. S. Georgia I., South Georgia Island; Bouvet I., Bouvet Island; S.O.I., South Orkney Islands.



cesses could have started about 27–25 MYA with a first split, possibly promoted by the formation of the Antarctic Convergence, which separated the Antarctic lineage (ancestor of *E. superba* and *E. crystallorophias*) from a sub-Antarctic one (ancestor of *E. vallentini* and *E. frigida*). A later split (7.9–7.2 MYA) that occurred within the sub-Antarctic stock gave rise to the latter two species. Considering that *E. frigida* is presently found only in Antarctic waters, we speculate that this species was able to disperse southward crossing the Antarctic Convergence.

If this hypothetical pattern holds true, it would indicate that isolation by the oceanographic barrier represented by the Antarctic Convergence is not the only force responsible for the speciation processes in euphausiids. In fact, the isolation favoured by the Antarctic Convergence cannot explain recent speciation events like the separation between *E. superba* and *E. crystallorophias* (3.1–2.8 MYA) or *E. vallentini* and *E. frigida* (7.9–7.2 MYA). Other factors, including those promoting sympatric speciation, could also be important. Hence, the present-day distribution appears, at least partly, to be the result of dispersal, suggesting that species with a similar life history may react to hydrographic barriers very differently. As a matter of fact, we cannot rule out that these four species (*E. superba*, *E. crystallorophias*, *E. frigida*, and *E. vallentini*) all originated in Antarctic waters and *E. vallentini* moved out afterward. In such a case, the Antarctic Convergence could have represented an oceanographic barrier for these species excluding *E. vallentini*.

Within-species analysis

Euphausia superba

Studies on *E. superba* at the population genetics level date back to the 1970s, the golden age of allozymes, when several investigations were aimed at testing for a positive correlation between genetic polymorphism and effective population size. The first investigation failed to find exceptionally high levels of heterozygosity in Antarctic krill, despite its large population size (Ayala et al. 1975). Nevertheless, it showed the existence of significant differences in allele frequencies at the phosphoglucose isomerase locus between samples collected near Anvers Island (Fig. 2) and samples from South Orkney Island and Bouvet Island (Fevolden and Ayala 1981). This report was supported shortly after by a similar finding of genetic differentiation between samples collected near Anvers Island and specimens obtained from west of the Antarctic Peninsula (cited in Fevolden and Schneppenheim 1989). Such findings were intriguing when considered in the light of krill distribution around Antarctica, which is characterized by areas of high and low abundance (Mackintosh 1973). The association of areas of high abundance with stable oceanic gyres suggested the possibility of a retention mechanism that

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Table 2. Number of *E. superba* individuals analyzed (*N*), haplotype diversity (*h*), and haplotype frequency in the populations investigated.

			Haplotype frequency										
Sample	*N*	*h*	A	B	C	D	E	F	G	H	I	L	Rare
South Georgia	70	0.823	0.40	0.01	0.13	0.01	0.01	0.01	0.03	0.04	0.06	0.04	0.26
Bellingshausen	63	0.852	0.35	0.03	0.09	0.00	0.00	0.00	0.02	0.06	0.06	0.13	0.26
Ross	48	0.827	0.35	0.02	0.10	0.00	0.00	0.04	0.00	0.04	0.04	0.15	0.26
Weddell	68	0.889	0.26	0.03	0.15	0.03	0.03	0.07	0.03	0.01	0.04	0.13	0.22

Note: Haplotypes with a frequency lower than 1% are pooled in the class "Rare."

could generate separate stocks of krill. However, as new samples were collected, the existence of population differentiation appeared to have no further support, and genetic homogeneity among krill populations was reported in a number of subsequent studies (Schneppenheim and McDonald 1984; Fevolden 1986; McDonald et al. 1986). Allozyme investigations did not find any global genetic differentiation (Fevolden and Schneppenheim 1989). The differences observed in the first studies (as well as some other occasional genetic heterogeneity detected for a few samples at some loci) were explained by technical problems such as difficulty in comparing allozyme data across laboratories and statistical artifacts (Fevolden and Schneppenheim 1989). However, other explanations such as localized nonrandom mating and selection acting on particular genes were not excluded (Fevolden and Schneppenheim 1989).

Recently, a population genetics investigation was carried out on *E. superba* at the DNA level by sequencing part of the ND1 gene (154 base pairs) in four population samples of 48–70 specimens collected in different sectors of the Antarctic Ocean (Fig. 2) (Zane et al. 1998). That study showed a remarkably high number of haplotypes (Table 2) and a significant genetic difference between South Georgia and East Weddell Sea samples, with a Φ_{st} value of 0.0213 ($P < 0.05$). Φ_{st} is analogous to F_{st} and measures the degree of genetic differentiation between populations while taking into account the sequence divergence between alleles (Excoffier et al. 1992). The distribution of the *P* values associated with the Φ_{st} pairwise statistics showed significant overall deviation from panmixia (following Manly 1984).

The fact that the genetic approach at the DNA level was capable of revealing the existence of a krill population structure over a limited number of samples (as compared with the protein polymorphism that failed to find differences on a much larger sample size) emphasizes the power of the molecular tool. At the same time, we cannot rule out that the present molecular approach could be limited with regard to detecting further genetic differences, considering that only a small number of nucleotides have been investigated (<200).

The difference found between the samples from South Georgia and East Weddell is interesting, considering that these two locations are separated by the Scotia–Weddell confluence, a well-known oceanic barrier that could restrict the gene flow, creating two isolated populations. On the other hand, marked fluctuations of krill abundance at South Georgia (Brierley et al. 1997) could be responsible for temporal rather than geographic differentiation. The fact that a limited number of samples were analyzed in Zane et al. (1998), together with the disadvantage that these were collected in different years, leaves the possible alternatives unresolved, stressing the need for specific repeated sampling in the area.

Analysis of the mtDNA data set also showed that Antarctic krill populations are not at mutation–drift equilibrium and are characterized by a pattern of molecular diversity compatible with a past population expansion that possibly occurred within the last 100 000 years. This result suggests a link between climatic changes and krill abundance (Zane et al. 1998). On the basis of the mtDNA data, it was also possible to approximate the female effective population size (since mtDNA is maternally inherited) to be between 264 000 and 415 000 individuals. Although this type of calculation tends to underestimate the "real" population size, this number appears to be extremely low if compared with a possible census size of 5×10^{14} individuals. This indicates that krill, despite the huge biomass, may be characterized by a limited effective population size and thus could be prone to genetic erosion.

Meganyctiphanes norvegica

Meganyctiphanes norvegica shows a wide distribution range and is present on the west and east sides of the North Atlantic Ocean as well as in the Mediterranean Sea. The interest for the population genetics of this species is relatively recent, as only a few papers have been published to date (Sundt and Fevolden 1996; Bucklin et al. 1997; Zane et al. 2000).

Protein polymorphism analysis of eight population samples collected in the Northeast Atlantic (Fig. 3) revealed genetic homogeneity and no population structure (Sundt and Fevolden 1996). A more recent study based on mtDNA markers examined Northwest Atlantic samples (Bucklin et al. 1997). In that study, one sample collected in Norwegian fjords was also included (Fig. 3). Part of two mitochondrial genes, cytochrome *b* and cytochrome oxidase I, were sequenced in approximately 100 individuals. The results of the overall haplotype frequency distribution were not compatible with a panmictic population. The deviation was found to be mainly associated with the Norwegian sample, whose haplotype frequency was determined to be significantly different from those of all the other samples. Instead, only a weak genetic difference was found within the northwestern samples, which was due to two samples collected at the same site (St. Lawrence estuary) during distinct years (temporal genetic variability).

In the framework of a European Union funded project (PEP project), the pattern of genetic differentiation in the Northeast Atlantic and Mediterranean has recently been investigated by SSCP and sequencing of part of the ND1 mitochondrial gene. Analysis of 385 individuals from eight population samples (Fig. 3) revealed a lower level of polymorphism in this species (Table 3) as compared with *E. superba* and strong deviation from panmixia (analysis of molecular variance, global $\Phi_{st} = 0.147$, $P < 0.01$) (Zane et al. 2000).

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Fig. 3. *Meganyctiphanes norvegica* sampling sites. Symbols indicate the population samples analyzed in different studies: triangles from Sundt and Fevolden (1996), squares from Bucklin et al. (1997), and circles from Zane et al. (2000). Arrows indicate the significant Φ_{st} and associated P values in a pairwise population comparison calculated from the data reported in Bucklin et al. (1997) (squares) and Zane et al. (2000) (circles).

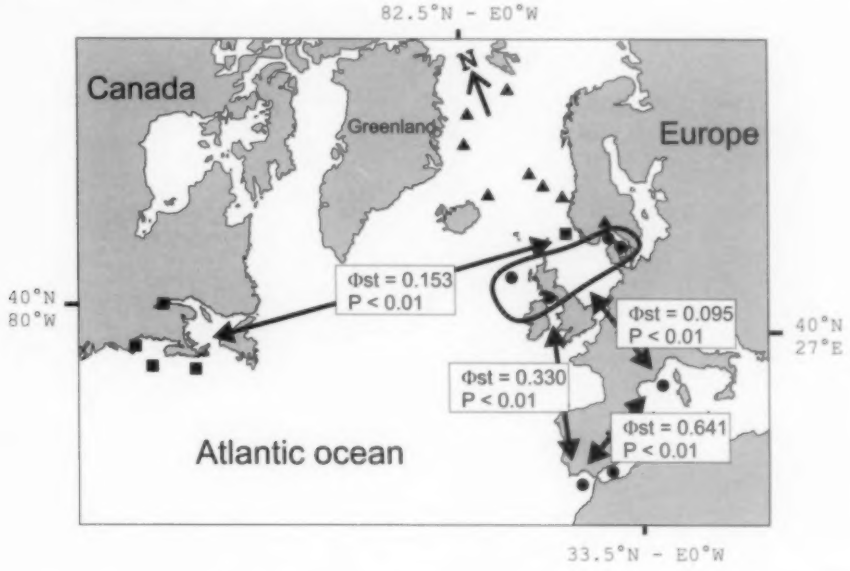

Table 3. Number of *M. norvegica* individuals analyzed (N), haplotype diversity (h), and haplotype frequency in the populations investigated.

			Haplotype frequency											
Sample	N	h	A	B	C	D	E	F	G	H	I	L	M	N
Kattegat, 1995	50	0.621	0.46	0.40								0.14		
Kattegat, 1996	49	0.559	0.53	0.41								0.06		
Skagerrak	47	0.589	0.49	0.43						0.02	0.02	0.04		
Rockall Trough	50	0.525	0.54	0.44			0.02							
Clyde	46	0.626	0.52	0.33	0.02							0.09	0.02	0.02
Alboran	46	0.445	0.70	0.28				0.02						
Ligurian	50	0.318	0.82	0.12	0.04	0.02								
Cadiz Bay	47	0.124	0.04	0.94					0.02					

This overall differentiation was largely due to two samples: that collected in Cadiz Bay (close to Gibraltar Strait but still in the Atlantic waters) and that collected in the Ligurian Sea (inside the Mediterranean). Both of these samples were found to be genetically divergent from all of the other populations ($\Phi_{st} = 0.330$, $P < 0.01$ for the Cadiz Bay population and $\Phi_{st} = 0.095$, $P < 0.01$ for the Ligurian population when compared with the remaining populations pooled together). On the other hand, the four Northeast Atlantic samples were found to be genetically homogeneous; moreover, the Kattegat population was shown to be homogeneous in two different years of collection (Zane et al. 2000).

The differentiation of the Ligurian sample could suggest the existence of a separated Mediterranean stock of *M. norvegica*, thus paralleling the pattern of genetic separation found in other nonpelagic invertebrates (Sanjuan et al. 1996, and references therein). This hypothesis could gain further support from the known demographic stability of the Ligurian population together with the recognized differences in ecology and ethology of this organism in the two areas (Atlantic and Mediterranean) (Cuzin-Roudy 1993; Cuzin-Roudy and Buchholz 1999). The Cadiz Bay sample, although collected in the Atlantic Ocean, was demonstrated to be the most genetically divergent sample investigated. Although explanations for such a finding are not straightforward, this result, together with the differences observed between Norway and the western Atlantic (Bucklin et al. 1997), indicates that *M. norvegica* may have a strong genetic structure with distinct genetic units within the same ocean, thus supporting the idea that some kind of oceanographic barrier may act in reducing the gene flow among different geographic areas.

General conclusions and future work

From the intraspecific data, a different picture emerges for northern krill as compared with Antarctic krill. While *E. superba* is characterized by weak genetic differentiation, *M. norvegica* is more structured, showing discrete genetic pools. This difference can be in part explained by the fact that the distribution of *M. norvegica* spans a larger geo-

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graphic area characterized by an oceanographic pattern that could actually restrict the gene flow between different regions. This holds true for the exchange between the western and eastern Atlantic as well as for the Atlantic–Mediterranean exchange. The Southern Ocean is, instead, characterized by strong circum-Antarctic currents that can provide extensive mixing of Antarctic waters, thus preventing strong population divergence of *E. superba*.

It should be restated, however, that in the past, this current might have represented a barrier to the gene flow, which could have favored the separation of the Antarctic stock of krill from the sub-Antarctic one. In both *E. superba* and *M. norvegica*, the present-day population structure appears to be complex, and the temporal stability of the observed differences is an important element to be tested by repeated sampling. Moreover, repeated sampling can provide a way to assess the effective population number at the species level because the variance in the allelic frequencies is inversely proportional to the effective population size (Hedgecock 1994; Li and Hedgecock 1998). Should the effective population turn out to be much smaller than the census size, this could have management implications for the conservation of the resource.

It should be noted that a complex social structure or social behavior could be responsible for temporal variation in allelic frequencies. To date, this element has been poorly addressed in population studies, probably because krill samples have often been collected on an opportunistic basis and detailed information about the investigated samples is rarely available. For instance, it would be important to know whether population samples are representative of a single swarm. In fact, comparing specimens belonging to the same or to different swarms (by the appropriate genetic tools) is certainly important in order to detect small-scale population substructuring. In conclusion, the genetic investigations carried out so far on krill provide good evidence that ocean currents may play an important role in shaping the present-day population structure of this pelagic organism. In addition, the phylogenetic analysis suggests that these currents might have promoted krill evolution by favoring allopatric speciation. However, further studies are needed at both the intraspecific and interspecific level to shed more light on the evolution of this fascinating organism.

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Effects of sea ice cover on the swarming behaviour of Antarctic krill, *Euphausia superba*

Andrew S. Brierley and Jonathan L. Watkins

Abstract: Much of the distribution range of Antarctic krill, *Euphausia superba*, is covered by permanent or seasonal sea ice. Sea ice extent has been implicated as a major factor affecting reproductive success of krill and krill dispersal, but little is known of the way in which ice cover may influence krill behaviour. This is largely because the under-ice environment is difficult to study. Ship-borne echosounders have, however, detected krill aggregations in midwater in ice-covered regions. We used 120-kHz echograms collected underway during three cruises that crossed ice-covered and adjacent open waters in the Bellingshausen, Weddell, and Scotia seas to compare morphological and next-neighbour characteristics of krill swarms within and without ice cover. No significant differences were detected between the horizontal and vertical extent of swarms or swarm next-neighbour distance in ice-covered or open waters. Distributions of swarm mid-depths did, however, differ significantly between ice-covered and open areas in all three seas, although the direction of difference was not the same in each instance: swarms in the Weddell and Scotia seas were generally shallower under ice than in open water, whereas in the Bellingshausen Sea the opposite prevailed.

Résumé : Une bonne partie de l'aire de répartition du krill antarctique, *Euphausia superba*, est couverte par des glaces de mer permanentes ou saisonnières. L'étendue de la glace de mer est considérée comme un facteur important qui agit sur le succès de reproduction du krill et sur sa dispersion, mais on sait peu de chose sur la façon dont la couverture de glace peut influer sur le comportement du krill, ce qui est dû en bonne partie au fait que l'environnement sous la glace est difficile à étudier. Des échosondeurs embarqués ont toutefois détecté des rassemblements de krill entre deux eaux dans les régions couvertes de glace. Nous nous sommes servis d'échogrammes de 120 kHz recueillis au cours de trois expéditions qui ont traversé des eaux couvertes de glace et des eaux libres adjacentes dans les mers de Bellingshausen, Weddell et Scotia pour comparer les caractéristiques morphologiques et de proximité des essaims de krill avec et sans couverture de glace. Aucune différence significative n'a été détectée dans l'étendue horizontale ou verticale des essaims, ni dans la distance la plus courte entre les essaims, dans les eaux couvertes de glace et les eaux libres. Les distributions de la mi-hauteur des essaims étaient toutefois nettement différentes selon que les eaux étaient couvertes ou non de glace dans les trois mers, mais la direction de la différence n'était pas la même dans chaque cas : les essaims des mers de Weddell et de Scotia étaient généralement situés moins loin sous la glace qu'en eau libre, alors que c'était le contraire dans la mer de Bellingshausen.

[Traduit par la Rédaction]

Introduction

Antarctic krill, *Euphausia superba*, form various types of aggregation (Kalinowski and Witek 1985) over a range of spatial and temporal scales (Murphy et al. 1988). The triggers for aggregation formation and the possible adaptive advantages of this biologically important phenomenon have been reviewed on a number of occasions (Miller and Hampton 1989; Siegel and Kalinowski 1994). The most obvious aggregation type is the "swarm" (Miller and Hampton 1989). Swarms have sharp boundaries and are typically tens of metres wide, several metres deep, contain thousands of krill per cubic metre, and have biomasses of tens to hundreds of tonnes fresh mass.

Much of the distribution range of Antarctic krill is covered by permanent or seasonal sea ice. Sea ice coverage around Antarctica varies seasonally between 4×10^6 km^2 in summer and 20×10^6 km^2 in winter (over half the Southern Ocean) (Gloersen et al. 1992) and is one of the largest and most dynamic ecosystems on earth. Sea ice has for some time been thought of as an important factor influencing the life cycle of Antarctic krill (Mackintosh 1972). More recently, sea ice extent has been implicated directly in the reproductive success and recruitment of krill (Siegel and Loeb 1995) and in mechanisms by which krill are dispersed through the Southern Ocean (Murphy et al. 1998*b*). However, sea ice is scarcely mentioned in reviews of krill swarming, and the mesoscale distribution of krill beneath ice is little known. This is because of the major difficulties associated with sampling beneath sea ice. SCUBA divers (e.g., O'Brien 1987) and remotely operated vehicles (Bergstrom et al. 1990) have only limited ranges and rarely deliver quantitative observations. There is some evidence of a marked change in sea ice extent around Antarctica in the mid-twentieth century (de la Mare 1997) and a growing belief that sea ice extent may continue to change because of regional climatic warming (e.g., Wu and Budd 1998). In order to understand how this may impinge upon the biology of

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krill, knowledge of the behaviour and distribution of the species in the ice environment is essential. New sampling approaches need to be developed to provide this knowledge.

For the past 20 years, acoustic surveys of krill abundance have been conducted at various locations around Antarctica (e.g., Brierley et al. 1999). In addition to providing data on regional abundance, underway fisheries acoustic survey data can be used to determine dimensions and densities of individual krill swarms (e.g., Miller et al. 1993). A small number of studies have reported properties of krill swarms from underway acoustic surveys in the vicinity of the ice edge (Sprong and Schalk 1992; Godlewska 1993) and from acoustic point observations in the ice itself (Daly and Macaulay 1988). To our knowledge, however, there are no published descriptions of morphology or spatial distributions of krill swarms detected acoustically underway in pack ice. We have found that the scientific echosounder system aboard the ice-strengthened RRS *James Clark Ross* can detect krill aggregations in midwater in ice-covered regions whilst the ship is underway: the transducers are recessed in the hull behind polycarbonate windows to protect them from ice damage and can be operated continuously even in heavy pack. Here, we examine acoustic data collected underway on transects in ice-covered regions of the Weddell, Bellingshausen, and Scotia seas and in neighbouring areas of open water in an attempt to describe influences of sea ice cover on krill swarm morphology and distribution. The cruises to the Weddell and Bellingshausen seas comprised transects through areas that could be classified easily as either ice covered or open water, and the transition between the two was clearly defined. The cruise to the Scotia Sea, in contrast, passed repeatedly through narrow bands of ice that were separated by tracts of open water. Data from these two different regimes enable the impact of ice cover on krill swarms to be investigated at two quite different scales.

Materials and methods

Study areas

Underway acoustic data were collected along mesoscale transects through neighbouring ice-covered and open waters during three biological science cruises aboard RRS *James Clark Ross*: cruise JR2 to the Bellingshausen Sea in 1992 (Turner and Owens 1995), cruise JR6 to the Weddell Sea in 1994 (White 1994), and cruise JR26 to the eastern Scotia Sea in 1997 (North et al. 1998). The cruise to the Bellingshausen Sea included a series of repeat transects along the 85°W line of longitude between October and December, during which time the ice edge was retreating southwards. The transect into the Weddell Sea ran from South Georgia towards Halley Bay in February. Ice was encountered in the Scotia Sea on the transect southeastwards from South Georgia to the South Sandwich Islands in November. Survey transects through the three study areas are shown in Fig. 1. Transects on all three cruises were effectively randomly placed with respect to the distribution of krill in a dynamic ocean environment (Trathan et al. 1993).

Acoustic data collection

Acoustic observations were made on all three cruises using a Simrad EK500 scientific echosounder driving a fully calibrated 120-kHz ES-120 transducer; 120 kHz is the frequency of choice for acoustic surveys of krill abundance and distribution (Everson and Miller 1994). The ES-120 transducer has a beam width of 9° and, on RRS *James Clark Ross*, an effective operating range of approximately 250 m. Ping repetition intervals were typically 1.5 s. Echograms were printed continuously ping-by-ping throughout each cruise and these paper records form the basis of the analysis reported here. Minimum echo intensity thresholds (S_v) on the 120-kHz echograms varied between –85 and –75 dB. Data were collected additionally at 38 kHz (all cruises) and 200 kHz (JR6, JR26).

Initial swarm measurements

Data on the size and position of acoustically detected krill swarms were extracted from the 120-kHz echograms in the first instance by direct measurement. Krill were distinguished from other sound scatterers by the appearance of their aggregations (Watkins and Brierley 2000) and characteristic difference in echo intensity at 120 and 38 kHz (Madureira et al. 1993). For the purposes of this analysis, a krill swarm was defined as any discrete target meeting the above criteria that, in addition, had a horizontal dimension on the echogram of at least 1 mm (approximately five pings) and was separated from any adjacent aggregation by at least two successive pings at both 120 and 38 kHz. For each swarm, horizontal width, vertical extent, mid-depth, and distance to the next swarm (or nearest ice edge for JR26) were measured to the nearest echogram millimetre. Swarm parameters were extracted only for aggregations observed during daylight hours because of the pronounced diel vertical migration and orientation changes exhibited by krill and the recognized impacts that these have on acoustic surveys at night (Demer and Hewitt 1995).

Correction for acoustic beam effects

Echograms provide a ping-by-ping record of the position and density of sound scatterers by depth range (*y*-axis) and time (*x*-axis) throughout a survey. With reference to vessel speed and sampling range, echogram measurements can be scaled to provide data on scatterer distribution in terms of distance traveled along the cruise track and depth. Extraction of aggregation dimensions from echograms is undertaken commonly to provide data on, for example, the size of fish schools (Massé et al. 1996), and an ICES study group has considered echogram analysis in detail (Reid 2000). One finding of this study group is that considerable caution must be exercised when converting echogram dimensions into true dimensions because of the shape and sensitivity of the echosounder beam: beam spreading, for example, results in targets detected at depth appearing to be wider than they actually are. We corrected swarm dimensions extracted from echograms for beam pattern effects using algorithms developed by Diner (1998), which take into account factors such as beam angle and echo detection threshold.

Analysis

Swarms were classified as being either under ice or in open water through reference to the ship's bridge navigation log and the 38-kHz echogram. The Officer of the Watch is required to record sea conditions every 3 h, and these observations provide a large-scale record of ice distribution. When the ship passes through ice-covered areas, noise spikes generated by ice scraping along the hull are apparent at 38 kHz and conveniently annotate the echogram with a fine-scale, real-time, underway record of ice location. Differences between the frequency distributions of swarm characteristics in open water and under ice were tested using the Kolmogorov–Smirnov two-sample test (Sokal and Rohlf 1995). This test is sensitive to differences in location, dispersion, and skewness between samples, and we used it here because we had no a priori reason to believe that it would simply be means or medians alone, for example, that might be different between samples. During cruise JR26, passage through many relatively narrow bands of ice separated by larger expanses of open water allowed multiple independent estimates of swarm parameters in open water to be

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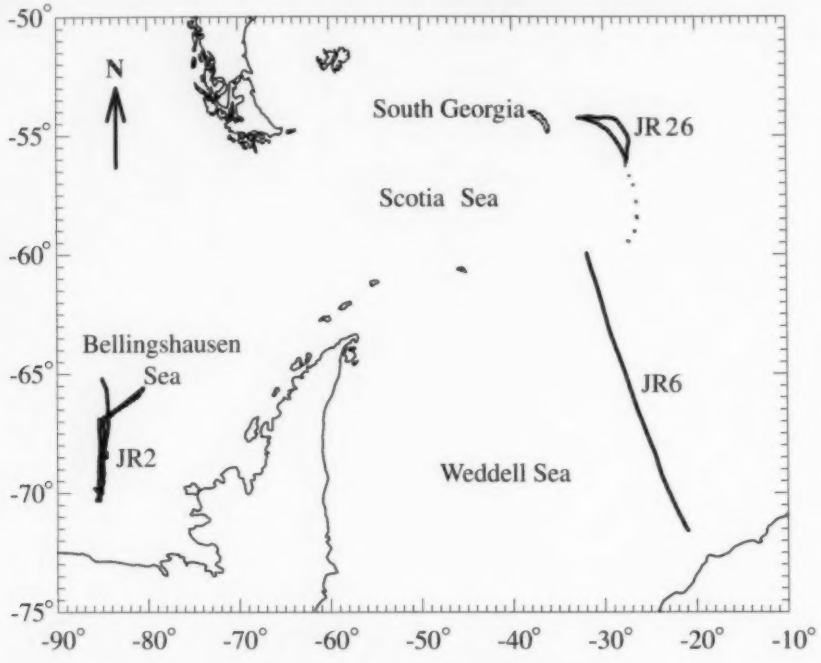
Fig. 1. Map showing acoustic survey transects through the Bellingshausen, Weddell, and Scotia seas.



obtained at varying ranges from ice edges. For this cruise, data for swarm characteristics that differed significantly between open water and ice-covered locations were examined swarm-by-swarm with reference to distance from ice in an attempt to determine the distance scale at which the presence of ice began to modify swarm behaviour.

Results

A combined total of 374 krill swarms were encountered during a little over 4500 km of transect. Maximum, minimum, and mean corrected dimensions of swarms within and without sea ice cover are given for each cruise in Table 1. A feature of the beam pattern correction algorithm is that it identifies those swarms that were too narrow to be properly ensonified (Diner 1998). These swarms had to be discarded from further analysis, reducing sample sizes (see Table 1).

Results of the Kolmogorov–Smirnov two-sample tests between frequency distributions of corrected swarm parameters are given in Table 1, from which it can be seen that most parameters measured did not differ significantly between ice-covered and open waters. The distributions of krill swarm mid-depths were, however, significantly different under ice and in open water in all three seas. In the Weddell and Scotia seas, krill swarms were shallower under ice, whereas in the Bellingshausen Sea they were shallower in open water. Histograms of swarm mid-depth distributions are shown in Fig. 2.

In an attempt to describe large-scale swarm dispersion, next-neighbour distances for swarms observed in the Bellingshausen and Weddell seas are given in Table 1. On both of these cruises, there was a very obvious geographical transition between open and ice-covered waters. By contrast, the transect across the Scotia Sea (JR26) passed repeatedly through narrow (typically <1 km) bands of ice. This ice distribution does not lend itself well to an investigation of swarm neighbour distance within and without ice. Neither do we consider that a simple summary of swarms per distance run within and without ice is a useful concept in this rapidly fluctuating, dynamic environment where ice bands were moving continually under the influence of winds. Instead, for this cruise, we have used the opportunity presented by repeated passes between ice-covered and open waters to look for evidence of change in swarm morphology over a smaller scale in proximity to ice. Swarm mid-depth was the only factor that differed significantly between under ice and open water ($P < 0.05$) (see Table 1), and a plot of swarm mid-depth against distance from ice is given for JR26 in Fig. 3. Swarm mid-depths of less than 50 m were only observed commonly within a horizontal distance of 250 m from ice edges.

Discussion

Findings reported here show clearly that acoustic data gathered on passage through sea ice can be used to evaluate quantitatively aspects of the swarming behaviour of Antarctic krill under ice. This is a valuable discovery in its own right, since it opens a much needed large-scale window of observation into an otherwise poorly described environment. Increasingly, it is being recognized that the Antarctic sea ice environment is of critical importance to the function of the entire Southern Ocean ecosystem, and understanding processes there is a priority.

While underway acoustic data can be used to make observations under ice, it is essential that analyses of acoustic data take proper account of echosounder system configura-

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Table 1. Comparison of swarm numbers and characteristics in ice-covered and open water, and results of Kolmogorov–Smirnov two-sample tests (D_{max}) between frequency distributions of swarm characteristics within and without ice-covered areas (*$P < 0.05$; **$P < 0.01$).

	Bellingshausen Sea (JR2)			Weddell Sea (JR6)			Scotia Sea (JR26)		
Swarm parameter	Under ice (782.8 km)	Open water (1016.8 km)	D_{max}	Under ice (368.1 km)	Open water (1186.8 km)	D_{max}	Under ice (total distance	Open water 1191.2 km)	D_{max}
Total no.	139	113		23	16		62	21	
No. after correction	118	107	—	23	16	—	62	20	—
No. for next neighbour analysis	133	108		22	15		—	—	
Horizontal extent (m)									
Max.	1 378.6	1 544.5		769.2	411.2		177.8	749.2	
Min.	0.7	0.7	0.15	34.5	55.7	0.16	3.7	10.8	0.34
Mean	89.6	135.8		152.0	107.1		65.1	115.8	
Vertical extent (m)									
Max.	150.0	177.5		27.8	35.4		35.0	72.5	
Min.	5.0	5.0	0.13	15.1	7.6	0.16	7.5	7.5	0.21
Mean	35.4	31.3		24.5	17.0		19.6	23.4	
Mid-depth (m)									
Max.	242.5	242.5		26.5	185.0		113.8	201.3	
Min.	13.8	10.0	0.35**	10.1	3.8	0.81**	17.5	7.5	0.36*
Mean	139.0	70.6		16.4	61.0		51.9	77.4	
Cross-sectional area (m^2)									
Max.	206 790.3	262 570.1		15 540.1	8 306.6		4582.3	35 586.0	
Min.	11.1	3.3	0.04	348.2	566.9	0.26	27.5	122.7	0.22
Mean	5 573.9	7 965.1		2 820.9	2 080.6		1388.6	3 655.2	
Next-neighbour distance (m)									
Max.	53 687.0	268 967.3		50 628.1	284 038.3				
Min.	47.5	12.4	0.04	53.8	80.6	0.04	—	—	—
Mean	5 641.2	9 141.9		6 319.4	36 177.5				

tions. Few previous acoustic studies of krill swarm dimensions report any attempts to correct echograms for beam pattern effects, although acoustic data have been used to draw conclusions about changes in krill swarm size in proximity to ice edges (see review in Godlewska 1993). If swarm width had not been corrected here, then we would have concluded that, for example, swarm widths in the Bellingshausen Sea were significantly different ($P < 0.05$) between ice-covered and open waters. This would have been an erroneous conclusion and demonstrates the importance of appropriate postprocessing.

The only swarm characteristic that differed significantly on all three cruises between ice-covered and open waters was swarm mid-depth. The response of swarms to ice cover was not the same in all instances, however; observations in the Weddell and Scotia seas (JR6 and JR26) showed swarms to be generally shallower under ice compared with open water, whereas observations in the Bellingshausen Sea during JR2 revealed the opposite: swarms were deeper under ice. The impact of ice cover on swarm distribution cannot therefore be considered as simple or uniform. Instead, sea ice is likely to mediate the interaction of a number of factors that modify krill behaviour, the relative importance of which may change through space and time. As in the open ocean, krill and other zooplankton under ice may seek an optimal balance between maximizing their potential to obtain food while at the same time minimizing their exposure to predation (Sih 1980; Daly and Macaulay 1991). Simplistically, this will involve krill swarms adjusting their depth to remain shallow enough to be able to exploit productivity in the euphotic zone (Priddle et al. 1997) but sufficiently deep for avoidance of visual predators (Hays 1994). Below, we seek to explain the apparent discrepancy in our observations of swarm depth in different seas in terms of feeding and predation.

One factor contributing to the apparent regional discrepancy in the response of krill swarm depths to ice cover may be the age and associated physical and biological properties of the sea ice encountered on the different cruises. Ice age is likely to be of major importance in determining the relationship between krill and the ice environment for at least two reasons. Firstly, the development of ice microalgal communities, a source of food for krill, progresses over time (Ackley and Sullivan 1994), and second-year ice has a more developed algal community associated with it than does first-year ice. In the Bellingshausen Sea, transects ran through a marginal ice zone of annual sea ice in the early stages of melting (Turner and Owens 1995), and most of the ice encountered was first-year ice (Aldworth 1995). In the Weddell Sea, by contrast, much of the ice was multi-year ice. The ice crossed during the cruise JR26 in the eastern Scotia Sea also had the appearance of multi-year ice (cf. Worby 1999). It is probable that this ice originated in the Weddell Sea. The South Sandwich Islands commonly form a barrier to ice drifting out of the Weddell Sea (S.F. Ackley, Clarkson University, U.S.A., personal communication), and, prior to the JR26 transect, there had been a sustained and consistently strong southerly wind that could have blown ice out of the Weddell Sea. If sea ice was the major source of food for krill in these locations, then it would be logical to

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Fig. 2. Frequency distributions of mid-depths of krill swarms observed beneath ice (circles) and in open water (squares) on transects through the (*a*) Bellingshausen, (*b*) Weddell, and (*c*) Scotia seas.

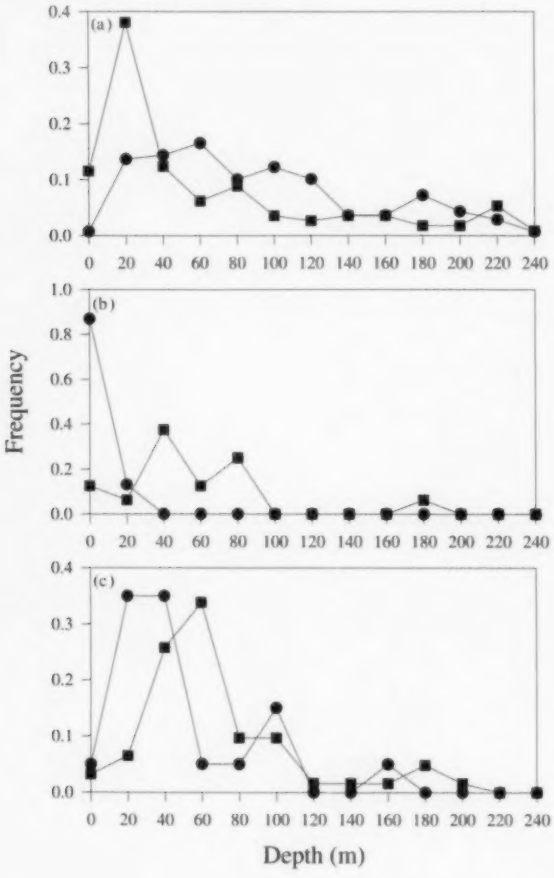
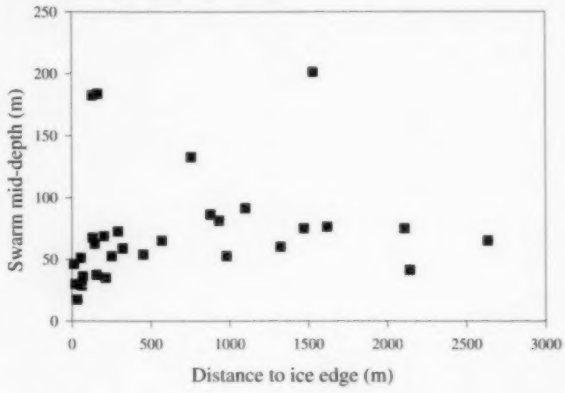


Fig. 3. Relationship between swarm mid-depth and range to ice edge on cruise JR26 (Scotia Sea).



expect the krill to maintain themselves in close proximity to it and therefore that krill in the Weddell and Scotia seas would be generally shallower under ice than in open water. Divers have reported a close association of krill with the immediate under-ice surface (O'Brien 1987) and the occurrence of large numbers of krill in ice interstices. Underway acoustic observations from ships will reveal little of processes at this small scale because of the disruptive nature of their passage through ice. However, krill must enter or leave the immediate under-ice environment from the pelagial (see Bergstrom et al. 1990), and it may be that animals making such a transition formed the bulk of swarms that we observed in shallower waters under ice in the Weddell and Bellingshausen seas. In the Bellingshausen Sea, swarms may have been shallower to the north of the ice edge because of the presence of a band of high surface chlorophyll (Turner and Owens 1995).

The second reason why sea ice age may influence the depth of underlying swarms is that older ice is generally thicker and has a more complex three-dimensional structure than first-year ice. Sea ice modifies the light regime in the underlying water column (Eicken 1992), and thicker ice (with a more well-established algal community) will attenuate light transmission to a greater extent than thinner (younger) ice. If, as has often been suggested, krill migrate to deeper (darker) waters in daylight hours to reduce their risk of detection by visual predators, then the generally reduced light intensities under older ice compared with younger ice would mean that krill beneath older ice would need to migrate less deeply to attain a given reduction in ambient light intensity. Furthermore, the more complex three-dimensional structure of older ice may offer krill a refuge from predators that is not available on the flatter undersurface of first-year ice. Krill beneath older ice may flee upward into ice interstices to evade predators rather than migrating downwards to regions of reduced light.

Observations in the Scotia Sea suggest that the influence of sea ice upon krill swarm depth is not restricted to the immediate ice environs. There is the suggestion in our data that krill swarms begin to adopt shallower depths up to a horizontal distance of 500 m from ice edges, although two outlying points detract from this apparent trend. Horizontal frontal gradients are associated with sea ice edges (Murphy et al. 1998*a*), forming as relatively fresh meltwater spreads outward from the edges, giving rise to strong stratification, and result in high-amplitude patchiness in phytoplankton abundance (Gosselin et al. 1986). It is possible, therefore, that krill swarms are responding to these frontal features and not to the ice edge itself (also see Daly and Macaulay 1991) and hence the distance offset. Alternatively, we may have observed small-scale temporal lag in behavioural response (depth change) to the movement of ice floes by wind. If floes are moved faster than krill can respond (vertically migrate), then a slight mismatch between swarm depth and ice cover is inevitable. It is important that biological and physical cause-and-effect relationships are examined on appropriate time and space scales (Steele and Henderson 1994) to avoid such aliases. Murphy et al. (1988) have reviewed the impacts of scale-dependent processes on krill.

Foraging and predation can be advocated as explanations of our observations of swarm distribution. However, the theory of optimal foraging upon which these explanations are based is not without challenge (e.g., Pierce and Ollason 1987) and this, combined with our generally poor under-

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standing of the under-ice environment, leaves the possibility that krill may be responding to other less well-known stimuli. It is also worthwhile remembering that all observations reported here were made in spring–summer. It has been suggested that the under-ice environment is of more importance to krill, particularly early larval stages, in winter months (Daly 1998) and our summer observations may not provide a true impression of the importance of ice to krill behaviour. Indeed, previous acoustic observations have suggested that krill migrate out from under ice into open waters in spring (Sprong and Schalk 1992). Observations in the winter months are needed to establish the overall importance of the sea ice environment to krill. Concurrent observations of ice structure will also be necessary to place biological observations in a robust environmental framework. As a final caveat, JR6 and JR26 took place in years of generally low krill abundance (Brierley and Watkins 1996; Brierley et al. 1999). Abundance estimates in the Bellingshausen Sea at the same time that cruise JR2 was conducted (but by a different ship, RRS *Discovery*) suggest that krill abundance was not abnormally low (Murray et al. 1995). Widespread observations in different seas in the same season would enable regional differences in characteristics of swarms within and without ice cover to be disentangled from the possible confounding influences of interannual variability in krill abundance.

This study has shown that underway acoustic observations from an ice-breaking research vessel can be used to make some quantitative measurements from krill swarms in ice-covered seas. As such, it offers a way to further considerably our understanding of krill behaviour in this unique environment. The disruptive nature of the passage of ships through ice, however, and the fact that the transducers are mounted in the ship's hull (depth 6 m) prevent data from being collected from the immediate ice–ocean interface, which may be critical for krill (Melnikov and Spiridonov 1996). The process of breaking ice also causes noise that might disturb swarms away from natural conditions (locational and morphological), leading to erroneous conclusions on the effect of ice cover on swarm morphology. Observations over the whole water column of swarms in an undisturbed state are required. Autonomous underwater vehicles (AUVs) have been proposed for this (Macaulay 1994) and now offer a viable platform from which to make these observations. AUVs have been deployed successfully under ice (Ferguson et al. 1999), and the United Kingdom's AUV *Autosub-1* has been designed with the ability to operate in this environment as a major objective (Millard et al. 1998). *Autosub-1* has been equipped with an EK500 echosounder (Fernandes et al. 2000) and is to be deployed from RRS *James Clark Ross* under Antarctic sea ice in the 2000–2001 austral summer. These missions may provide the first large-scale observations of krill swarms under ice in an undisturbed state and should offer clear insight into the behaviour of the species in this environment, which appears to be of critical importance to it.

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Fatty acid composition as an indicator of carnivory in Antarctic krill, *Euphausia superba*

G.C. Cripps and A. Atkinson

Abstract: In a previous study at South Georgia, carnivory was invoked as a cause of high polyunsaturated fatty acid (PUFA) content of Antarctic krill, *Euphausia superba*. To examine this, krill were sampled and fed for 16 days exclusively on the locally abundant copepod *Drepanopus forcipatus*. After 16 days, the krill had increased their PUFA content from 28 to 54% of the total fatty acids. Concurrently, monounsaturated fatty acids (MUFAs) and saturated fatty acids (SFAs) decreased from 41 to 27%. Thus, the krill appeared to accumulate PUFAs as reflected in their diet of *D. forcipatus*, which also had a relatively high PUFA content (50%). Overall, the results support omnivorous feeding by krill at South Georgia during nonbloom periods. We propose that the ratio of PUFA to SFA content may be used to detect carnivory in the recent feeding history of krill and suggest that this may be an index which could be applied to other zooplankton.

Résumé : Dans une précédente étude menée à l'île de Géorgie du sud, la forte teneur du krill antarctique, *Euphausia superba*, en acides gras polyinsaturés (AGPI) a été reliée à l'alimentation carnivore de ce crustacé. Pour examiner la question, nous avons prélevé du krill que nous avons nourri exclusivement pendant 16 jours avec le copépode localement abondant *Drepanopus forcipatus*. Après 16 jours, le krill avait accru sa teneur en AGPI, qui était passée de 28% à 54% des acides gras totaux. En parallèle, la teneur en acides gras monoinsaturés (AGMI) et en acides gras saturés (AGS) avait baissé, passant de 41% à 27%. Le krill semblait donc accumuler des AGPI grâce à sa consommation de *D. forcipatus*, qui présente aussi une teneur relativement élevée en AGPI (50%). Globalement, les résultats appuient l'alimentation omnivore du krill autour de la Géorgie du sud pendant les périodes de non-prolifération planctonique. Nous suggérons d'utiliser le rapport des AGPI aux AGS pour détecter une phase récente d'alimentation carnivore chez le krill, et cet indice pourrait s'appliquer à d'autres organismes zooplanctoniques.

[Traduit par la Rédaction]

Introduction

Throughout the Southern Ocean, the phytoplankton population is characterised as a background of low biomass, composed of small diatoms and flagellates, upon which blooms of large diatoms are superimposed (Smetacek et al. 1990; Clarke and Leakey 1996). These blooms provide abundant food for krill and other grazing zooplankton. However, as the phytoplankton is uneven in quality and quantity, krill can resort to carnivory (Price et al. 1988; Atkinson and Snÿder 1997). The extent to which krill change to alternative food sources is open to debate (Quetin and Ross 1991) and may vary regionally. Krill appear to be able to utilise whatever food is available (Schnack 1985) and have physiological mechanisms to enable them to survive periods when food is scarce (Ikeda and Dixon 1982; Quetin and Ross 1991; Hagen et al. 1996). It has been suggested that krill feed omnivorously during nonbloom periods around the island of South Georgia. This conclusion was based on feeding experiments (Atkinson and Snÿder 1997), the low algal carbon rations derived from gut fluorescence (Pakhomov et al. 1997), and lipid biomarker analysis (Cripps et al. 1999)

The analysis of lipids in marine zooplankton can aid the interpretation of trophic interactions, particularly when the lipids retain a signature of their dietary origin. This approach has been applied to Antarctic zooplankton using fatty acid signatures by, for example, Graeve et al. (1994*a*) and Cripps and Hill (1998). These signatures have been used to distinguish between herbivorous and omnivorous Antarctic copepods (Graeve et al. 1994*a*) and to follow diet-induced changes in polar copepods (Graeve et al. 1994*b*; Kattner et al. 1994).

Virtue et al. (1993) found changes in the fatty acid profiles of Antarctic krill, *Euphausia superba*, when fed controlled algal diets in the laboratory, from which they suggested that biochemical signatures were related to the food sources. As some variation in lipid composition of krill with age and sex has been recorded (Pond et al. 1995; Mayzaud et al. 1998), variation in the fatty acid composition might also be expected. Indeed, differences between maturity stages and sex in krill were observed by Clarke (1980) and Virtue et al. (1996). However, more recently, Cripps et al. (1999) reported that changes in fatty acid content, presumably due to diet, can obscure differences due to sexual maturity.

Fatty acid composition is a potentially valuable indicator of diet. In previous work on krill from South Georgia in 1996 (Cripps et al. 1999), a high proportion of polyunsaturated fatty acids (PUFAs) compared with saturated fatty acids (SFAs) in one group of krill was suggested to have

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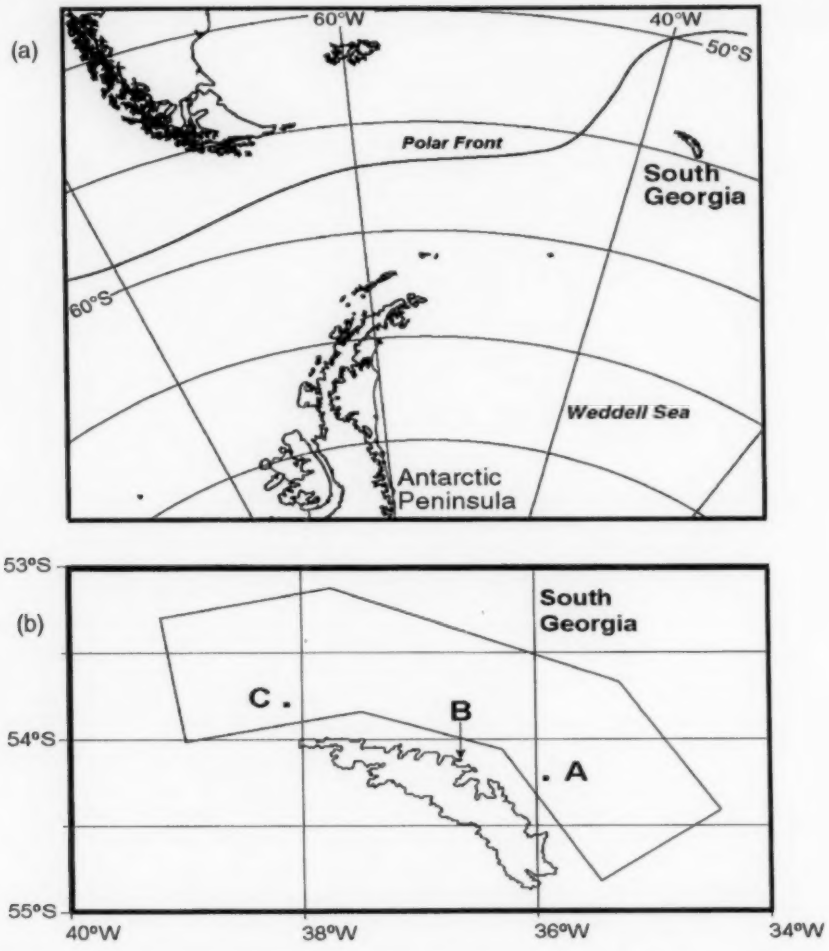
Fig. 1. (*a*) South Georgia in relation to the Antarctic Peninsula and the approximate position of the Antarctic Polar Front and (*b*) the study area and sample sites at South Georgia.



resulted from a diet of copepods. In order to draw firmer conclusions, an experiment was set up to investigate how a pure diet of locally caught copepods would affect the fatty acid signature of krill. The fatty acid signatures of these purely carnivorous krill were then compared with those of krill from 1996, krill caught from a region high in diatom biomass, and other zooplankton also from South Georgia with various dietary habits. The results are used to discuss the utility of this biomarker method and the PUFA/SFA ratio as an index of in situ diet in krill at South Georgia.

Materials and methods

Experimental

Krill and other zooplankton were sampled from the region of the Southern Ocean to the north of South Georgia (Fig. 1) in the austral summer of January 1998. Live krill were caught with slow, near-surface net hauls (nominal opening 1 m^2) over the northern shelf at site A (Fig. 1), and other krill and zooplankton were collected at a number of sites within the study area. This included site C, a region where phytoplankton were dominated by large diatoms (>20 μm). These animals were sampled from oblique hauls of a rectangular midwater trawl (nominal opening 8 m^2) and vertical bongo net hauls deployed from the RRS *James Clark Ross* to a depth of 100 m. Samples were stored at –80°C for 6 months until analysis. *Drepanopus forcipatus*, the copepods used in the feeding experiment (see below), were caught by vertically hauled nets from a depth of 20 m in Stromness Bay, a fjord on the northern coast of the island (site B).

A small number of krill collected from site A (N = 25) were kept alive in a 50-L carboy and fed exclusively on a diet of copepods over a period of 16 days. The animals were initially acclimatised to laboratory conditions for 24 h and then subjected to an alternating cycle of food and no food. During the feeding periods, the krill were fed excess quantities of *D. forcipatus* (approximately 1 g carbon·m^{-3}). For the first 2 h of this cycle, the krill were fed with live *D. forcipatus* and then were fed for 22 h with freeze-killed *D. forcipatus*, which was followed by 24 h without food in filtered seawater. This cycle was repeated eight times in total.

The rationale for using this cycle and using freeze-killed *D. forcipatus* was that the animals were being used in parallel for an excretion experiment (Atkinson and Whitehouse 2000). While *D. forcipatus* may not be a standard dietary item for the large ma-

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Table 1. Summary of fatty acids in the experimental Antarctic krill *E. superba* compared with diet and krill from a previous study in 1996 (Cripps et al. 1999).

	16:1[*n*–7]/16:0 ratio	18:1[*n*–7]/18:1[*n*–9] ratio	% SFA	% MUFA	% PUFA	PUFA/SFA ratio
Phytoplankton from krill sampling site (one sample)	0.39	0.29	79	17	4	0.05
Krill feeding on diatoms (one sample of 20 animals)	0.43	0.82	36	27	37	1.03
Krill at the start of the experiment (mean of 10 animals)	0.48	0.54	41	31	28	0.68
Krill experimental animals after 16 days (mean of 10 animals)	0.46	0.63	27	19	54	2.00
Drepanopus forcipatus (one sample, 50 animals)	0.64	0.23	23	27	50	2.17
Krill: carnivorous animals from 1996 (mean of 11 samples of 20 animals)	0.93	0.67	13	22	65	5.00

jority of the Southern Ocean krill population, the South Georgia region appears to be atypical. *Drepanopus forcipatus* are locally very numerous over the extensive continental shelf around South Georgia (Hardy and Gunther 1935; Atkinson and Peck 1990) and are likely to be a major target for omnivorous and carnivorous zooplankton. These copepods were of the same size range (1–3 mm) as those cleared at maximum rates, based on the experiments on krill and food from these waters by Atkinson and Snÿder (1997). Thus, *D. forcipatus* was a valid species for use in the experiment.

The fact that the krill were feeding at very high rates on freeze-killed food as well as live food was demonstrated by their very high ingestion rates. The mean daily ration of freeze-killed copepods was estimated at 32% of body mass per day (range 21–43%). This corresponded to the maximum rates previously reported for krill (see Quetin et al. 1994). At the end of the 16-day period, the krill were stored at –80°C. Samples of *D. forcipatus*, the initial experimental animals from site A, krill feeding on the diatom-dominated phytoplankton at site C, and the phytoplankton at C were also taken for fatty acid analysis.

Analysis

The analytical protocols were based on established procedures (Christie 1982). In brief, individual krill from the experiment and bulked samples of other zooplankton (see Table 1 and the Appendix for sample size and replication) were homogenised in a chloroform–methanol (2:1) mixture and the resulting chloroform extract was concentrated under a stream of nitrogen and then dissolved in methanolic potassium hydroxide and refluxed to effect saponification. Fatty acids were extracted from the resulting liquor in hexane and the fatty acid methyl esters were then prepared by refluxing the hexane concentrate in methanolic hydrochloric acid. The fatty acid methyl ester (FAME) fraction was then extracted into hexane and purified on an Isolute® silica solid-phase extraction cartridge (Cripps and Tarling 1997). The FAME fraction was analysed by capillary gas chromatography using a suite of analytical standards (Sigma Chemical Co. and Supelco Inc.) on an HP4890A gas chromatograph fitted with a HP Innowax® 25-m analytical column (0.2 mm internal diameter, 0.33 µm film thickness), splitless injection, and flame ionisation detection. The column temperature was programmed after an initial period of 1 min at 40°C to 150°C at 55°C·min^{-1}, then to 250°C at 2.5°C·min^{-1}, and finally held at 250°C for a further 20 min. Structural confirmation of the FAMEs was by gas chromatography – mass spectrometry at the Natural Environmental Research Council supported mass spectroscopy facility at the Organic Geochemistry Unit, University of Bristol.

Results and discussion

Accumulation of PUFAs in krill feeding on copepods

Krill fresh from the sea at the start of the experiment had a pattern of fatty acids similar to that of the krill feeding on a diatom bloom at site C (Fig. 2). After 16 days of a copepod diet, their percent content of PUFA 20:5[*n*–3] increased from 14 to 28% and 22:6[*n*–3] from 6 to 17%. The concentrations of these particular fatty acids also increased from 1 to 5.5 mg·g fresh mass^{-1} and from 2 to 9 mg·g fresh mass^{-1}, respectively. The total fatty acid concentration increased, but the pattern of monounsaturated fatty acids (MUFAs) and SFAs showed little variation, with small increases in the 16:1[*n*–7]/16:0 and 18:1[*n*–7]/18:1[*n*–9] ratios (Table 1). Thus, the krill accumulated PUFAs 20:5[*n*–3] and 22:6[*n*–3] from their diet of copepods but not in any particular preference to MUFAs, SFAs, or other unsaturated compounds such as 16:4[*n*–3] and 18:4[*n*–3]. Although the high ingestion rates of the freeze-killed food could reflect superfluous feeding and decreased assimilation rates, the rapid change in the composition of the fatty acids suggests that large amounts of food were being consumed.

Comparison with krill from 1996 at South Georgia

The experimental krill increased their PUFA content over a relatively short period. Their 20:5[*n*–3] percentage was comparable to that of the field krill caught from South Georgia in 1996, which were thought to be starving or resorting to carnivory (Fig. 2) (Cripps et al. 1999). The available phytoplankton during most of the 1996 study was lower than during the present study, and the difference between the fatty acid profiles of the freshly caught krill from the two seasons reflects this (Fig. 2). The krill from 1996 may have been under dietary stress for a number of weeks rather than days and had probably not been consuming only the species used in the experiment, *D. forcipatus*. The 16:4[*n*–3] present in the 1996 krill may have come from other copepods, e.g., *Calanoides acutus* and *Rhincalanus gigas*, also found in the ocean around South Georgia (Appendix). These species may have provided the 1996 krill with higher proportions of 16:1[*n*–7] and 18:4[*n*–3] compared with the experimental krill. Nevertheless, the pattern of the apparently

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Fig. 2. Fatty acid patterns of (*a*) diatoms from site C, (*b*) Antarctic krill feeding on diatoms from site C, (*c*) carnivorous krill from 1996 (Cripps et al. 1999), (*d*) krill at the start of the experiment, (*e*) experimental krill after 16 days, and (*f*) *D. forcipatus*, the copepod species from site B fed to the krill during the experiment.

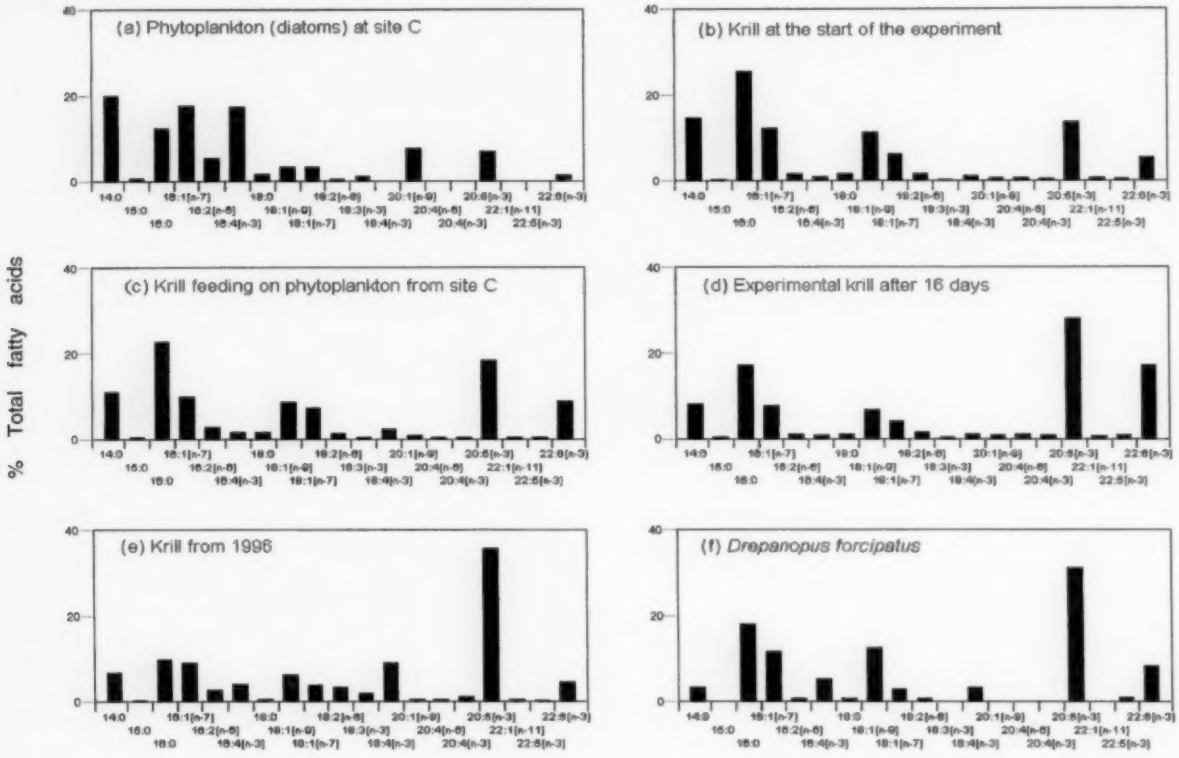
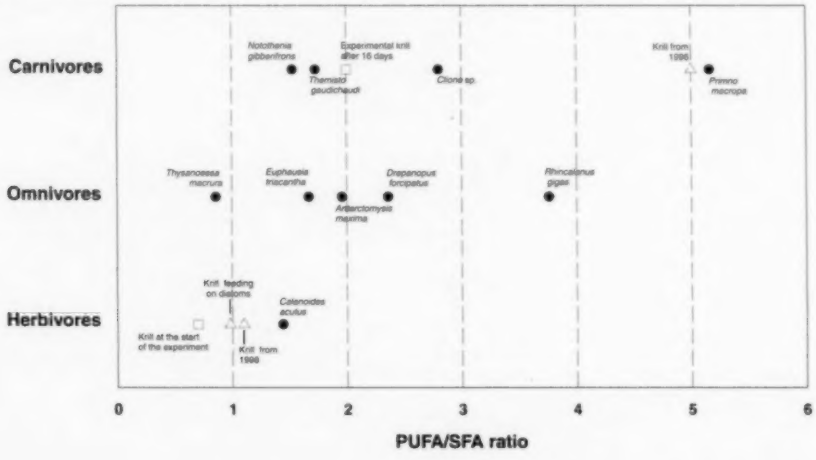

% Total fatty acids
(a) Phytoplankton (diatoms) at site C
(b) Krill at the start of the experiment
(c) Krill feeding on phytoplankton from site C
(d) Experimental krill after 16 days
(e) Krill from 1996
(f) Drepanopus forcipatus

Fig. 3. PUFA/SFA ratios in the Antarctic krill used in the experiment (□) and krill from the field (△) compared with other pelagic zooplankton (●) from South Georgia.



omnivorous/carnivorous krill from 1996 (Cripps et al. 1999) was significantly different from that of krill known to have been feeding in regions of high diatom biomass in this study (Fig. 2) and others (e.g., Cripps and Hill 1998).

Although krill fatty acids appear to change in relation to their diet, our data suggest that some important dietary acids may be preferentially assimilated. This was apparent from krill feeding on phytoplankton at site C (Fig. 2). The phyto-

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plankton generally contains less PUFAs than any of the herbivorous or carnivorous zooplankton, and it is only the large diatoms (>20 μm) that contain substantial quantities of PUFA. Although the diatom-rich phytoplankton from site C was high in PUFA (33% of total fatty acids), only 8% of this was 20:5[*n*–3] and 22:6[*n*–3]. The 20:5[*n*–3] and 22:6[*n*–3] PUFAs appeared to be assimilated by the krill in preference to MUFAs, SFAs, and the PUFA 16:4[*n*–3]. However, the krill accumulated more 20:5[*n*–3] and 22:6[*n*–3] PUFAs when feeding on the copepod *D. forcipatus* than the krill feeding on phytoplankton (diatoms) at site C. Thus, the fatty acid composition of krill feeding on *D. forcipatus* and subsequent high PUFA content were a reflection of diet.

A high PUFA proportion may also indicate starvation due to the depletion of triglycerides, as polar lipids (e.g., phospholipids) have much higher PUFA levels compared with triglycerides (Clarke 1980). Thus, a high PUFA content may be deceptive without separate analyses of phospholipids and triglycerides. However, our experiment showed that there was an increase in PUFAs on both absolute and relative scales.

PUFA/SFA ratio as an index of carnivory in krill

The PUFA/SFA ratio increased in krill after being fed a carnivorous diet over a period of 16 days. The krill at the beginning of the experiment and those that had been feeding on phytoplankton, which was essentially diatoms, at site C had low PUFA/SFA ratios (<1.0). This was similar to the exclusive herbivore analysed, *C. acutus* (Falk-Petersen et al. 1999), and the lower end of the range for the omnivorous species (Fig. 3). The mean value for krill throughout the study area was also low at 1.1 (Appendix), suggesting general herbivory in krill at the time of our sampling. After 16 days, the krill in the experiment had increased their PUFA/SFA ratio to 2.0, which was in the lower half of the range for the carnivorous species and similar to that of their prey, *D. forcipatus* (2.17). The krill from 1996 were found to have a PUFA/SFA ratio of 5.0, which was at the top of the range for carnivorous species and may reflect the differences in the copepods (or other prey) that they fed on. There was a measure of overlap in the ranges of the PUFA/SFA ratio between carnivores and omnivores. However, we propose that the ratio of PUFAs to SFAs is a useful indicator of carnivorous feeding in krill and suggest that it may be extended to other euphausiids with similar diets, such as *Euphausia triacantha* and *Thysanöessa macrura*. Some further calibrations may be necessary, but this method in conjunction with other observations can provide insights into the recent feeding history of krill and can provide useful seasonal and regional comparisons. The experimental results support the suggestion that the high 20:5[*n*–3] and other PUFA content of krill during the 1996 study (Cripps et al. 1999) resulted from omnivorous or carnivorous feeding.

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Appendix. Percent fatty acid composition of the total lipid extract of zooplankton and fish larvae from South Georgia, January 1998.

	Calanoides acutus (stage CV)	*Drepanopus forcipatus* (stages CIV–CVI)	*Rhincalanus gigas* (stage CVI)	*Clione* sp.*	*Antarctomysis maxima*	*Primno macropa*	*Themisto gaudichaudii*	*Euphausia superba*	*Euphausia triacantha*	*Thysanöessa macrura*	*Notothenia gibberifrons* (larvae)
Analyses of *N* individuals	10 (*N* = 25)	1 (*N* = 50)	10 (*N* = 25)	1 (*N* = 30)	1 (*N* = 15)	1 (*N* = 20)	8 (*N* = 40)	13 (*N* = 20)	3 (*N* = 20)	2 (*N* = 40)	1 (*N* = 20)
Fatty acid											
14:0	9.2	3.3	1.2	2.4	4.0	1.7	3.7	11.2	4.8	17.7	6.6
15:0	—	—	—	6.8	0.2	0.1	0.8	0.4	0.6	0.3	0.3
16:0	12.1	18.1	6.6	7.5	14.1	8.3	13.5	22.2	15.2	21.9	19.3
16:1[*n*–7]	23.9	11.5	23.9	12.9	6.3	7.4	8.2	9.7	7.9	5.5	9.7
16:2[*n*–6]	1.5	0.8	3.2	1.8	—	0.7	0.6	2.0	—	0.8	1.1
16:4[*n*–3]	2.0	5.2	1.4	0.4	1.3	3.3	1.4	1.0	0.7	0.6	2.6
18:0	0.9	0.8	0.4	0.8	1.0	0.7	1.2	1.3	1.0	0.7	1.8
18:1[*n*–9]	6.9	12.6	29.8	2.4	19.7	9.1	10.2	8.7	15.5	8.6	10.8
18:1[*n*–7]	1.2	1.4	5.3	3.9	6.4	3.2	4.8	6.0	9.1	6.1	3.2
18:2[*n*–6]	3.3	2.9	2.0	0.7	1.0	1.5	1.3	1.9	1.2	1.1	1.0
18:3[*n*–3]	0.6	—	0.6	0.5	0.3	0.4	0.6	0.6	0.4	0.4	0.3
18:4[*n*–3]	5.1	3.3	6.0	1.7	2.4	2.8	2.4	1.4	1.4	0.7	3.1
20:1[*n*–9]	11.5	—	1.7	1.9	8.9	11.2	7.8	1.0	7.6	2.8	4.8
20:4[*n*–6]	—	—	0.3	0.7	0.5	0.7	0.7	0.6	0.6	0.3	0.4
20:4[*n*–3]	0.7	—	0.1	1.0	0.8	0.8	0.9	0.6	0.7	0.4	0.5
20:5[*n*–3]	17.3	30.9	15.9	20.9	17.5	28.4	23.3	19.7	15.9	20.6	18.7
22:1[*n*–11]	1.4	—	—	—	1.9	2.5	1.6	0.7	2.1	1.2	0.9
22:5[*n*–3]	—	0.9	—	1.2	0.7	1.2	1.0	0.5	0.8	0.6	1.0
22:6[*n*–3]	2.3	8.3	1.4	13.8	13.2	16.2	16.2	10.6	14.6	9.8	14.0
PUFA/SFA ratio	**1.4**	**2.4**	**3.8**	**2.8**	**2.0**	**5.2**	**1.7**	**1.1**	**1.7**	**0.9**	**1.5**
16:1[*n*–77]/16:0	2.0	0.6	3.6	1.7	0.5	0.9	0.6	0.4	0.5	0.3	0.5
18:1[*n*–7]/18:1[n–9]	0.2	0.1	0.2	1.6	0.3	0.4	0.5	0.7	0.6	0.7	0.3

*The composition of *Clione* sp. also included fatty acids 17:0 (3.6%) and 17:1[*n*–8] (15:1%).

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An optimisation model of the diel vertical migration of northern krill (*Meganyctiphanes norvegica*) in the Clyde Sea and the Kattegat

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Abstract: An optimisation model was developed to examine the effect of predation risk and environmental conditions on the diel vertical migration (DVM) of adult northern krill (*Meganyctiphanes norvegica*). Model predictions were compared in two locations with contrasting environmental conditions, the Clyde Sea and the Kattegat. The model was constructed from a combination of parameterised functions and empirical field data obtained during summer conditions. Parameter matrices were set up to cover the entire water column over a 24-h period. The first matrix contained values for "net energy gain," which incorporated empirical data on temperature-dependent respiration, copepod and phytoplankton abundance, and a functional response model for feeding rate. The second matrix expressed the risk of encountering a generalised visual (fish) predator as a function of light levels. The optimisation procedure sought a path through depth and time such that the energy gain was equal to the amount necessary to grow, produce eggs, and moult, while the risk of predation was minimised. The model predicted DVM in both the Clyde Sea and the Kattegat. Sensitivity analyses showed that the predicted DVM pattern was mainly driven by food and predation risk, with temperature effects on metabolic costs having a minor effect.

Résumé : Nous avons élaboré un modèle d'optimisation pour examiner les effets du risque de prédation et des conditions environnementales sur la migration verticale nycthémérale du krill nordique (*Meganyctiphanes norvegica*) adulte. Les prédictions du modèle ont été comparées à deux endroits présentant des conditions environnementales très différentes, la mer de Clyde et le Kattegat. Le modèle a été construit à partir d'une combinaison de fonctions paramétrisées et de données empiriques de terrain obtenues dans des conditions estivales. Les matrices des paramètres ont été établies de façon à couvrir l'ensemble de la colonne d'eau sur une période de 24 h. La première matrice contenait des valeurs correspondant au « gain énergétique net » qui intégraient les données empiriques sur la respiration dépendante de la température, l'abondance des copépodes et du phytoplancton et un modèle de réaction fonctionnelle pour le taux d'alimentation. La deuxième matrice exprimait le risque de rencontrer un prédateur visuellement généralisé (poisson) en fonction du niveau d'éclairement. La procédure d'optimisation a formulé un cheminement dans la profondeur et dans le temps de façon que le gain énergétique soit égal à la quantité nécessaire pour la croissance, la production d'oeufs et la mue, tandis que le risque de prédation était minimisé. Le modèle a prédit la migration verticale nycthémérale en mer de Clyde et dans le Kattegat. Des analyses de sensibilité ont montré que le patron de migration prédit était essentiellement régi par l'alimentation et le risque de prédation, les effets de la température sur les coûts métaboliques n'ayant qu'un effet mineur.

Introduction

Diel vertical migration (DVM) behaviour is a regular pattern of behaviour that is widespread in the zooplankton community, occurring in all oceans at both high and low latitudes (Longhurst 1976). The pattern of migration mainly varies between a normal DVM, where animals ascend to the upper layers at nighttime and descend to deeper layers during the day, and reverse DVM, where ascent is during daytime and descent during the night. Midnight sinking is a commonly observed phenomenon (Tarling et al. 1999 and references therein) where individuals that have migrated to the surface during the evening sink down slowly during the course of the night. There are also many zooplankton spe-

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cies that do not show any type of vertical migration behaviour as well as others in which vertical migration becomes increasingly pronounced during the course of the life cycle (see review by Angel 1985).

Many theories have been put forward as to the cause of vertical migration. One of the earliest postulated that vertical migration afforded escape from predation (Russell 1927). This has been elegantly demonstrated by more recent work that found that species performing the behaviour were more successful in situations where visual fish predators were introduced into lakes (e.g., Zaret and Suffern 1976). This is supported by marine examples where DVM was more apparent during periods when the abundance of visual fish predators was seasonally high (e.g., Bollens and Frost 1989). Field evidence that food concentration influences DVM is not as strong, although the laboratory studies of Johnson and Jakobsen (1987) on *Daphnia longispina* and Huntley and Brooks (1982) on *Calanus pacifica* demonstrated that the behaviour may be modified or even stopped under certain food conditions. The clear relationship between respiration rate and temperature (see Ikeda 1985) suggests an adaptive value in moving up and down vertical temperature gradients in order to gain maximum metabolic advantage (McLaren 1963), although this is contested by more recent modelling studies (e.g., Ohman 1990).

Behavioural strategies that maximise fitness often involve trade-offs (Krebs and Davies 1991), and it has been shown in numerous studies that animals sacrifice food intake in the face of potential danger (e.g., Gilliam and Fraser 1987). With respect to the vertical positioning of zooplankton, this trade-off will vary through a diel cycle as changing light levels alter predator capture ability and prey vulnerability (Mangel and Clark 1988). For modelling purposes, it is necessary to consider such a trade-off quantitatively so that the fitness consequences of foraging and danger can be assessed. The approach taken in this investigation follows that of Gilliam and Fraser (1987) where a forager chooses patches with the lowest ratio of mortality rate to feeding rate subject to the constraint that the feeding rate is above the level required to survive. The advantage of the approach is in its use of ratios that allow application to situations where an absolute quantitative assessment of certain environmental parameters may not be possible. This is because optimal habitats are decided by the general rule

(1) Prefer habitat A to B if: $E_A / E_B < H_A / H_B$

where E is predation risk and H is energy gain, such that the rule depends only on the relative level of mortality and intake in the two sites, not on the absolute levels.

The euphausiid northern krill (*Meganyctiphanes norvegica*) exhibits a pronounced DVM throughout its wide geographical range, which includes the North Atlantic and Arctic oceans and Mediterranean Sea. It feeds on a combination of phytoplankton and copepods depending on their seasonal availability (Mauchline 1960) and is a major part of the diets of pelagic fish such as herring and bottom-dwelling fish such as cod (Tanasichuck 1999). Its wide range of habitats results in separated populations that appear to be adapted to quite contrasting sets of abiotic and biotic conditions. The optimal DVM strategy in such contrasting situations may differ considerably. Comparing predicted DVM patterns against those observed in the field for locations with contrasting environmental conditions is therefore a powerful validation procedure and a good test of the robustness of the model's design.

Northern krill populations in the Clyde Sea and the Kattegat were sites of a major recent investigation (PEP programme; see Acknowledgements and Buchholz et al. 1998) where information was collected on the trophic environment and hydrographic conditions as well as the vertical migration behaviour, respiration rate, and feeding behaviour of northern krill in summer environmental conditions. It was apparent that environmental conditions did differ between the two sites, as did the exact pattern of vertical migration. Through running the model with these different sets of parameter values, the aim was twofold. Firstly, it was to determine whether the model was robust and able to predict a DVM pattern that was close to field observations in contrasting environments. Secondly, it was envisaged that the comparison of the sites, as well as further sensitivity analyses, would identify those parameters that were of greatest importance to producing the predicted patterns.

Material and methods

Structure of the model

The model predicts the vertical migration behaviour of krill over a 24-h period in a summer situation. The water column is divided into intervals of between 10 and 20 m (j) and time into hourly periods (i). A parameter matrix of the energy gain (H) of occupying each of these depth–time cells is calculated by taking away the respiration costs (M_{ij}) of occupying the cell from the expected food intake (F_{ij}) (i.e., $H = I - M$) to give a give a matrix of the form $\{H_{ij}\}$. Correspondingly, a mortality risk matrix of the form $\{E_{ij}\}$ is calculated as a function of light and the visual range of the predator. The model is run iteratively to find a vertical distribution pattern that minimises the total mortality risk over the 24-h period while gaining enough energy to meet the daily demands of growth, moulting, and reproduction. Symbols, definitions, and units for all parameters used in the model are given in Table 1.

Parameters for calculating energy gain (H)

Respiration rate

Respiration rate (M) may be parameterised as a function of temperature and weight in the general form

(2) $M = aW^b$

where a is a scaling coefficient, b is the weight-specific exponent for respiration, and W is weight (for zooplankton examples, see Ikeda and Motoda 1978). Stuart (1986) estimated the weight exponent b as 0.845. Temperature dependence of krill respiration was investigated in onboard experiments carried out on the R/V *Heincke* during visits to the Clyde Sea and the Kattegat (Saborowski et al. 2000). Results were combined with those of Stuart (1986) to give the following equation for the hourly respiration rate:

(3) $M = 0.020334(0.4389 + 0.08938T)W^{0.845}$

where M is respiration rate and W is dry weight (DW). This was converted to energy assuming that 1 L O_2 respired = 20332 J (Winberg 1971).

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Table 1. Symbols, definitions, and units for the parameters used in the model.

Symbol	Definition	Units	Value
j	Depth zone	m	
i	Time interval	h	
H_{ij}	Hourly energy gain	J·h^{-1}	
H_t	Daily energy gain	J·day^{-1}	
M, M_{ij}	Respiration rate	µL O_2·h^{-1}	
F	Expected food intake	µg DW·h^{-1}	
E_{ij}	Mortality risk		
a	Scaling coefficient dependent on temperature	µL O_2·mg^{-1}·h^{-1}	
b	Weight-specific exponent for respiration		
W	Weight (DW)	mg	
T	Temperature	°C	
G	Copepod ingestion rate	µg DW·h^{-1}	
C	Copepod biomass	µg DW·L^{-1}	
P	Proportion of phytoplankton to total energy intake		
Chl a	Concentration of Chl a in the environment	mg·L^{-1}	
S	Assimilation efficiency		0.8
e	Encounter rate	h^{-1}	
v	Fish velocity	m·h^{-1}	50
N	Fish density	Individuals·m^{-3}	
dt	Time interval	1 h	
θ	Field of view (upward-looking fish)		0.5
r	Visual range	m	
z	Depth	m	
c_z	Local beam attenuation coefficient	m^{-1}	
K	Local diffuse attenuation coefficient	m^{-1}	
ρ	Light fraction lost at the surface		0.5
I_s	Irradiance at the surface	µmol·m^{-2}·s^{-1}	
C_0	Inherent contrast of krill		0.5
A_{zp}	Krill cross-sectional area	m^2	0.0000126
ΔS_e	Sensitivity of planktivore eye	µmol·m^{-2}·s^{-1}	3.0 ×10^{-6}

Ingestion rate: copepods

A copepod ingestion rate equation was developed from the works of McClatchie (1985) and Båmstedt and Karlson (1998). McClatchie (1985) incubated Northern krill in copepod concentrations ranging from 200 to 4000 µg DW·L^{-1} and calculated a functional response curve for the hourly ingestion rate of copepods (G):

$$(4) \qquad \log_{10}G = 0.746\log_{10}C - 0.686$$

where C is copepod biomass. McClatchie (1985) predicted that relatively high concentrations of copepods were necessary (2265 µg DW·L^{-1}) to meet metabolic demands. Båmstedt and Karlson (1998) found that much lower concentrations of copepods were adequate (145 µg DW·L^{-1}). The major difference between the two studies was the size of the incubation chambers (4 L in the former study and 45–90 L in the latter), with the larger chambers used by Båmstedt and Karlson (1998) making them less likely to suppress ingestion rates compared with the McClatchie (1985) study. However, Båmstedt and Karlson (1998) did not expose krill to different concentrations of copepods in order to calculate a functional response curve. Here, we make the assumption that the suppression of ingestion was constant at all concentrations of copepods and adopt the functional response curve of McClatchie (1985). The y intercept of McClatchie's (1985) equation was altered so that the curve intercepts the hourly ingestion rate given by Båmstedt and Karlson (1998) at the copepod concentrations that they used; hence, the hourly ingestion rate becomes

$$(5) \qquad \log_{10}G = 0.746\log_{10}C + 1.092.$$

Ingestion rate was converted to joules assuming that 1000 µg DW copepod material = 26 J (Omori and Ikeda 1984).

Ingestion rate: phytoplankton

Phytoplankton supplements the mainly carnivorous diet of northern krill (e.g. McClatchie 1985; Båmstedt and Karlson 1998). Nevertheless, the amount of chlorophyll pigment in the guts becomes relatively high when krill enter phytoplankton-rich layers (see Mauchline 1960). In the Clyde Sea in July 1996, for instance, chlorophyll a (Chl a) was relatively high at 16.15 mg·L^{-1} between 20 and 10 m (Table 2). Krill showed a diel cycle in the Chl a pigment content in their guts, peaking during the night at around 4 µg Chl a·individual^{-1} and dropping to virtually nothing during the day (P. Mayzaud, unpublished data). Given a gut transit time of 60 min (P. Mayzaud, unpublished data), this gives a total daily intake of 20 µg Chl a·individual^{-1}, equivalent to 23.5 J of energy assimilated (assuming an assimilation efficiency (S) of 0.8; Lasker 1966). This is approximately half of the daily energy requirement that we have calculated for an average-sized adult krill in the Clyde during summer (43 J for a 93 mg DW krill at 9°C).

At concentrations at or above 16.15 mg Chl a·L^{-1}, phytoplankton feeding is assumed to meet half the daily metabolic requirement of the individual such that net energy gain per hour becomes

$$(6) \qquad H_{ij} = \frac{(G_{ij}S) - (1 - P_{ij})M_{ij}}{1 - P_{ij}}$$

where

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Table 2. Average Chl *a* concentration and copepod biomass at midday and midnight in defined depth intervals in the Clyde Sea and the Kattegat.

Clyde Sea depth interval (m)	Chl *a* ($mg \cdot L^{-1}$)	Daytime biomass ($\mu g \cdot L^{-1}$)	Nightime biomass ($\mu g \cdot L^{-1}$)	Kattegat depth interval (m)	Daytime biomass ($\mu g \cdot L^{-1}$)	Nightime biomass ($\mu g \cdot L^{-1}$)
10–0	16.12	3.10	14.20	20–0	12.54	21.91
20–10	16.15	2.64	32.94	40–20	15.72	3.05
40–20	10.71	8.09	5.04	60–40	12.42	11.70
60–40	4.78	5.17	0.24	80–60	7.12	9.85
80–60	1.85	1.27	0.37	100–80	15.13	9.76
100–80	0.80	0.24	0.32	115–100	14.42	15.55
120–100	0.95	0.06	0.19			
135–120	1.10	0.12	0.35			

$$(7) \qquad P_{ij} = 0.5\left[\frac{\text{Chl } a}{16.15}\right]$$

and Chl *a* is equal to the concentration of phytoplankton (milligrams per litre). This means that where the concentration of Chl *a* is below the maximum level, i.e., 16.15 $mg \cdot L^{-1}$, the relative hourly contribution from phytoplankton feeding to the total energy intake becomes reduced in a linear fashion.

Parameters for calculating expected probability of mortality (*E*)

Visual predation

Visual fish predators were assumed to be the principal source of mortality of krill in the upper layer water column of the Clyde Sea and the Kattegat (Tanasichuck 1999). The expectation that a krill will encounter a fish in the upper layers (e) is calculated as a function of visual range (r), speed (v), and density of the predator (N) and the size of the prey (following Eggers 1977):

$$(8) \qquad e = \theta \pi r^2 v N dt$$

where θ is the field of view of the fish and dt is the time interval (other units as in Table 1).

It is assumed that each encounter (e) results in death of the krill prey, so the expectation of mortality (E) of an individual krill may be calculated as

$$(9) \qquad E = 1 - \exp(-ed).$$

The parameter E is a probability function so that, if scaled up to the population level, the value would represent the proportion of individuals lost to the population per unit time as a result of visual predation. Predator visual range r is obtained from an equation developed by Aksnes and Giske (1993) and may be calculated through a Newton–Raphson iteration:

$$(10) \qquad r^2 \exp(c_z r + zK) = \rho I_s |C_0| A_{zp} \Delta S_e^{-1}$$

where z is depth, c_z is the local beam attenuation coefficient, K is the local diffuse attenuation coefficient, ρ is the light fraction lost at the surface (0.5; Aksnes and Giske 1993), I_s is the irradiance at the surface, C_0 is the inherent contrast of krill (0.5; Aksnes and Giske 1993), A_{zp} is the krill cross-sectional area, and ΔS_e is the sensitivity of the eye of the planktivore (3.0×10^{-6} $\mu mol \cdot m^{-2} \cdot s^{-1}$; Rosland and Giske 1994). Values for the parameters are given in Table 1.

Tactile predation

In the deeper layers where visual predation levels are extremely low, it is believed that that bottom-dwelling tactile fish predators such as cod add marginally to the level of E, given the high levels of northern krill found in cod stomachs (F. Buchholz, unpublished data). This factor was built in through increasing the calculated level of visual predation by two orders of magnitude in the deepest layer and by one order of magnitude in the next layer up. Furthermore, the level of visual predation in these layers was not allowed to decrease below the level observed at 12:00.

Production requirements of krill

According to Lasker (1966), the percentage investments from assimilated energy for *Euphausia pacifica* were as follows: respiration, 67%; growth, 9%; reproduction, 9%; moulting, 15%. If the respiration rate of the krill is known, then the energy demand for growth, reproduction, and moulting can be inferred. In eq. 3, respiration was a function of temperature and body size. Given that temperature varies with depth, total energy respired over a 24-h period will depend on the exact vertical migration behaviour. The vertical migration profile is nevertheless an output of the model, while growth, reproduction, and moulting represent energy targets to be fixed at initial parameterisation. To use the relationship provided by Lasker (1966) in order to estimate the amount of energy required for growth, reproduction, and moulting, therefore, it was necessary to infer an average temperature occupied by krill over a 24-h period. In both the Clyde Sea and the Kattegat, field data indicated that the average depth occupied when considering the mean of the daytime and nighttime distributions was approximately 70 m. At this depth, the temperature was 9.2°C in the Clyde Sea and 6.2°C in the Kattegat. Body size was set at the modal size-class of the adult population, which was 39 mm (93 mg DW) in the Clyde Sea and 34 mm (6.154 mg DW) in the Kattegat (G.A. Tarling, unpublished data). The resulting value for the hourly respiration rate, provided by eq. 3, was converted to daily respiration rate through multiplication by 24. Daily rates for growth, reproduction, and moulting were then calculated as proportions of daily respiration rate following the values given by Lasker (1966) and presented in Table 3.

Environmental data sets

Energy gain (H)

Data used to calculate the energy budget are principally taken from sampling missions carried out during July and August 1996 in the Clyde Sea and the Kattegat onboard R/V *Heincke*. Depth-discrete estimates of Chl *a* profiles and copepod biomass are presented in Table 2 and are described further in Lass (1998). The copepod data in Table 2 were obtained from midnight and midday net deployments, and these were assumed to be representative of daytime and nighttime situations. To simulate the transition period between these two situations, a sliding mean function was applied to the dusk (20:00–22:00) and dawn (04:00–06:00) periods. Temperature profiles are presented in Fig. 1.

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Table 3. Daily rates of energy demand for growth, reproduction, and moulting as proportions of respiration rate in the Clyde Sea and the Kattegat following the proportional values given in Lasker (1966).

	Respiration ($J \cdot day^{-1}$)	Growth ($J \cdot day^{-1}$)	Reproduction ($J \cdot day^{-1}$)	Moulting ($J \cdot day^{-1}$)	Total energy demand ($J \cdot day^{-1}$)
Clyde Sea	28.6	3.8	3.8	6.4	42.7
Kattegat	14.3	1.9	1.9	3.2	21.3

Fig. 1. Typical temperature profile of (*a*) the Clyde Sea and (*b*) the Kattegat during summer environmental conditions (April–May and July 1996).

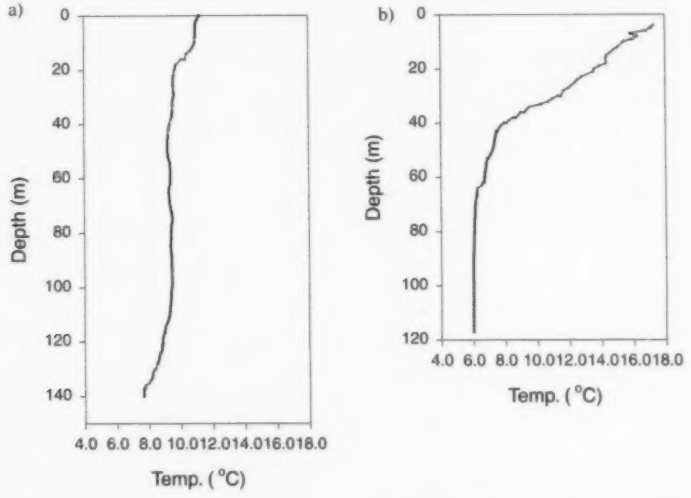
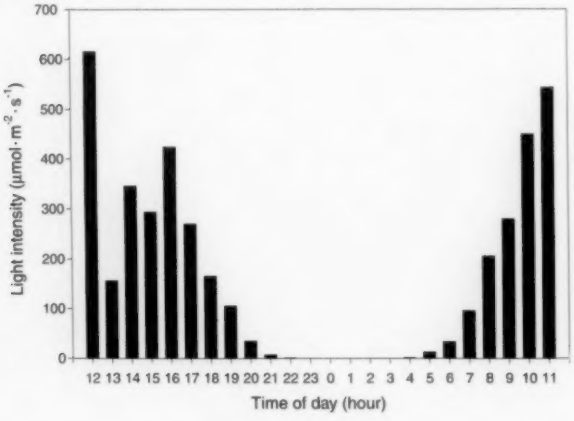


Fig. 2. Light intensity profile used in the Clyde Sea and Kattegat models taken from a typical day during the PEP programme summer sampling mission.



Expectation of mortality (E)

Levels of irradiance were taken from a typical 24-h period during the Clyde Sea and Kattegat sampling missions using data from the irradiance meter onboard R/V *Heincke* (Fig. 2) (note that absolute values were found to be offset, so both data sets were reset to a peak value of 98 μeinsteins·m^{-2}·s^{-1}). The attenuation coefficient (K) was measured at 0.2881 in the Clyde Sea and 0.1213 in the Kattegat using a diffuse-light transmissometer. The c_z is assumed to be three times K. A value of 0.01·m^{-3} was taken as the fish density in the Clyde Sea and 0.001·m^{-3} as that in the Kattegat. The implications of setting these fish density values are explored in the sensitivity analyses.

Parameter matrices

The parameter matrices $\{H_{ij}\}$ and $\{E_{ij}\}$ for the Clyde Sea consisted of eight depth intervals (j) covering a 135-m water column. For the Kattegat, there were six depth intervals (j) covering a 115-m water column. The total time period was 24 h in both environments, divided into hourly intervals (i). The net energy balance (H) for each cell (ij) was calculated as follows according to eq. 6.

Model run procedure

At the start of the model run, a net energy gain target for the 24-h period (H_t) is set such that it is equal to the daily requirement to grow (g), reproduce (s), and moult (w) such that

$$(11) \quad H_t = g + s + w$$

(see Table 3 for values of g, s, and w). An iteration procedure (Microsoft Excel 97 Solver: Generalized Reduced Gradient (GRG2) nonlinear optimization) is run until the optimal solution to the following problem is found under the constraint that the krill must spend and cannot exceed 1 h in each of the 24 time intervals (i) such that

$$(12) \quad \sum_{i=1}^{i=24} H_{ij} > H_t \text{ and } \sum_{i=1}^{i=24} E_{ij} = \min E.$$

For the Clyde Sea, H_t was set at 14 $J \cdot day^{-1}$, while for the Kattegat, it was 7 $J \cdot day^{-1}$ (see Table 3).

No constraint is placed on the animal with respect to moving from one depth interval to any other between time intervals.

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Tarling et al. (1998*a*) observed upward swimming speeds above 7 cm·s^{-1} and downward swimming speeds as high as 11 cm·s^{-1} in northern krill in the Mediterranean Sea. This would equate to a total distance travelled of 252 m upwards and 396 m downwards per hour. These distances are twice as great as the depth of the water column at either of the study sites and illustrate that this animal is capable of rapid movement between any of the depth intervals defined in this model. A further assumption is that there is no additional metabolic cost in moving between depth intervals. This assumption is based on the work of Kils (1981), who showed that Antarctic krill (*Euphausia superba*) are capable of swimming at speeds of up to 15 cm·s^{-1} without affecting their standard metabolism. This is because krill regulate their speed mainly by changes in the execution of the pleopod swimming stroke. At 15 cm·s^{-1}, the stroke is maximally executed. Above 15 cm·s^{-1}, stroke frequency must be increased, which then raises metabolic rate to an "active metabolism." Northern krill, although smaller, have the same basic design as Antarctic krill, and it is believed that the reduction in propulsive force from the comparatively smaller pleopods is counteracted by a corresponding decrease in the resistance of the body moving through the water, since both parameters are a function of the surface area. To achieve upward rather than horizontal swimming, krill must change their body angle so that most of the propulsive force is projected into the vertical rather than the horizontal vector, in much the same way as an aerofoil (Kils 1981). A rise in standard metabolism is therefore not expected at the rate of movement between depth intervals predicted by the model, and so only standard metabolic rates are used in model parameterisations.

Results

Parameter matrices

The energy budget matrix calculated for the Clyde Sea is presented in Fig. 3*a* and for the Kattegat in Fig. 3*b*. For the Clyde Sea, depth intervals below 60 m have a negative energy balance at any time of day as a result of the low food availability and hence low energy intake that cannot compensate for the cost of respiration. Above this depth, the energy balance is mostly positive, although there is variation according to time of day as the copepod biomass migrates out of one depth interval and into another.

For the Kattegat, the energy balance is almost wholly positive at any depth, with the deepest depth interval being the most profitable in terms of energy gain. Furthermore, this depth layer does not oscillate in terms of energy balance over the 24-h period, since the relatively high copepod biomass remains at a steady level. Closer to the surface, it is apparent that some layers are more profitable during daytime and that other layers are more profitable at night as the copepod community performs DVM. The 40- to 20-m layer, for instance, switches from being a relatively high-profit depth interval during daytime to a slightly negative environment at night, while the reverse occurs between 20 m and the surface.

Values for each cell (*ij*) in the expectation of mortality matrix were obtained from the calculation of eqs. 10, 8, and then 7. The resulting matrix for the Clyde Sea is shown in Fig. 3*c* and for the Kattegat in Fig. 3*d*. In the Clyde Sea during daytime, it is apparent that depth intervals above 20 m have values for E that are many orders of magnitude greater than those below 20 m. During night, this difference drops to within three orders of magnitude. It should also be noted that although the deepest depth intervals have been altered to include the effect of bottom-feeding fish, visual predation remains the dominant influence on the general shape of the expectation of mortality matrix. The expectation of mortality matrix in the Kattegat has the same general shape as in the Clyde Sea, although the lower K in the Kattegat makes values of E comparatively higher at deeper depth intervals.

Optimal time allocations

The optimal time allocation within the depth–time matrix under the given constraints for the Clyde Sea is presented in Fig. 4*a*. It is apparent that the krill have a daytime depth of between 60 and 40 m during most of the daytime period. At 22:00, they begin an upward migration into the 40- to 20-m depth interval and then enter the 20- to 10-m layer after 01:00 where they remain until 04:00. By 06:00, the krill have returned to their daytime depth between 60 and 40 m.

In Fig. 5*a*, the rate at which energy is gained (H_t' per hour) is compared with the expected rate of mortality E (per hour). For most of the daytime period, H_t' is close to zero or even slightly negative. The principal period of H_t' is during nighttime, which corresponds to the period when the krill occupy depth intervals that are closer to the surface. Between 01:00 and 04:00, H_t' values are up to 6 J·h^{-1}. Correspondingly, this period is also the time when the krill experience their E, rising from a daytime level of close to zero to 0.000269·h^{-1}. The net H_t' from this optimal time allocation strategy was equal to the target H_t (14 J·day^{-1}). The E was 0.000994·day^{-1}. Details on the division between copepod and phytoplankton ingestion and the cost of respiration are presented in Table 4.

The optimal time allocation strategy for the Kattegat under the given constraints is presented in Fig. 6*a*. Krill occupied the 100- to 80-m depth interval for the midday period (11:00–16:00) but otherwise spent the majority of their time between 80 and 60 m. The only other movement predicted was into the 60- to 40-m depth interval between 04:00 and 05:00. In Fig. 5*b*, it is apparent that H_t' was relatively steady and positive over the entire 24-h period. The highest rates of around 1.5 J·h^{-1} corresponded to the occupation of the 100- to 80-m depth interval between 11:00 and 16:00 and also the brief movement into the 60- to 40-m depth interval at 04:00. The lowest rates of 0.5 J·h^{-1} corresponded to the time spent in the 80- to 60-m depth interval. Values for E showed a marked difference between day and night, with values as high as 0.0012·h^{-1} being experienced between 11:00 and 16:00, while nighttime values were close to zero.

The net H_t' from this optimal time allocation strategy was higher (19.42 J·day^{-1}) than the target H_t (7 J·day^{-1}). The E was 0.009082·day^{-1}. Details on the division between copepod and phytoplankton ingestion and the cost of respiration are presented in Table 4.

Sensitivity analyses

Predation levels

The density of predators in the original runs of the model were assigned as 0.01·m^{-3} in the Clyde Sea and 0.001·m^{-3} in the Kattegat, since these densities produced values for E within an order of magnitude of the mortality rate of 0.0003·day^{-1} (i.e., the proportion lost to the population each day) that was predicted for northern krill by Labat and

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Fig. 3. Depth–time matrices (covering the entire water column over a 24-h period) of the net energy gain in (*a*) the Clyde Sea and (*b*) the Kattegat and the expected mortality rate (as a proportion of the population) in (*c*) the Clyde Sea and (*d*) the Kattegat. Each matrix cell covers a depth interval of between 10 and 20 m and a time period of 1 h.

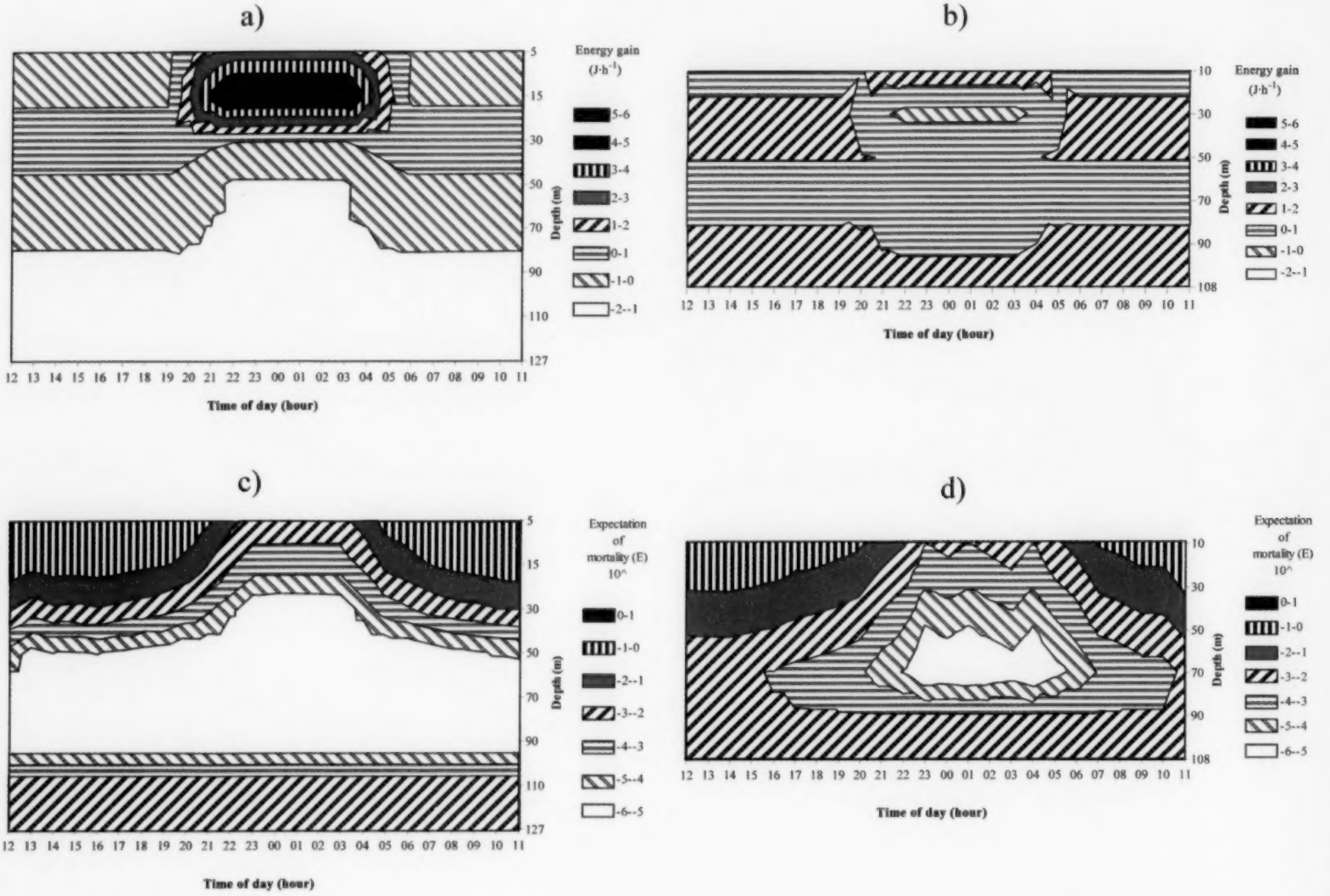

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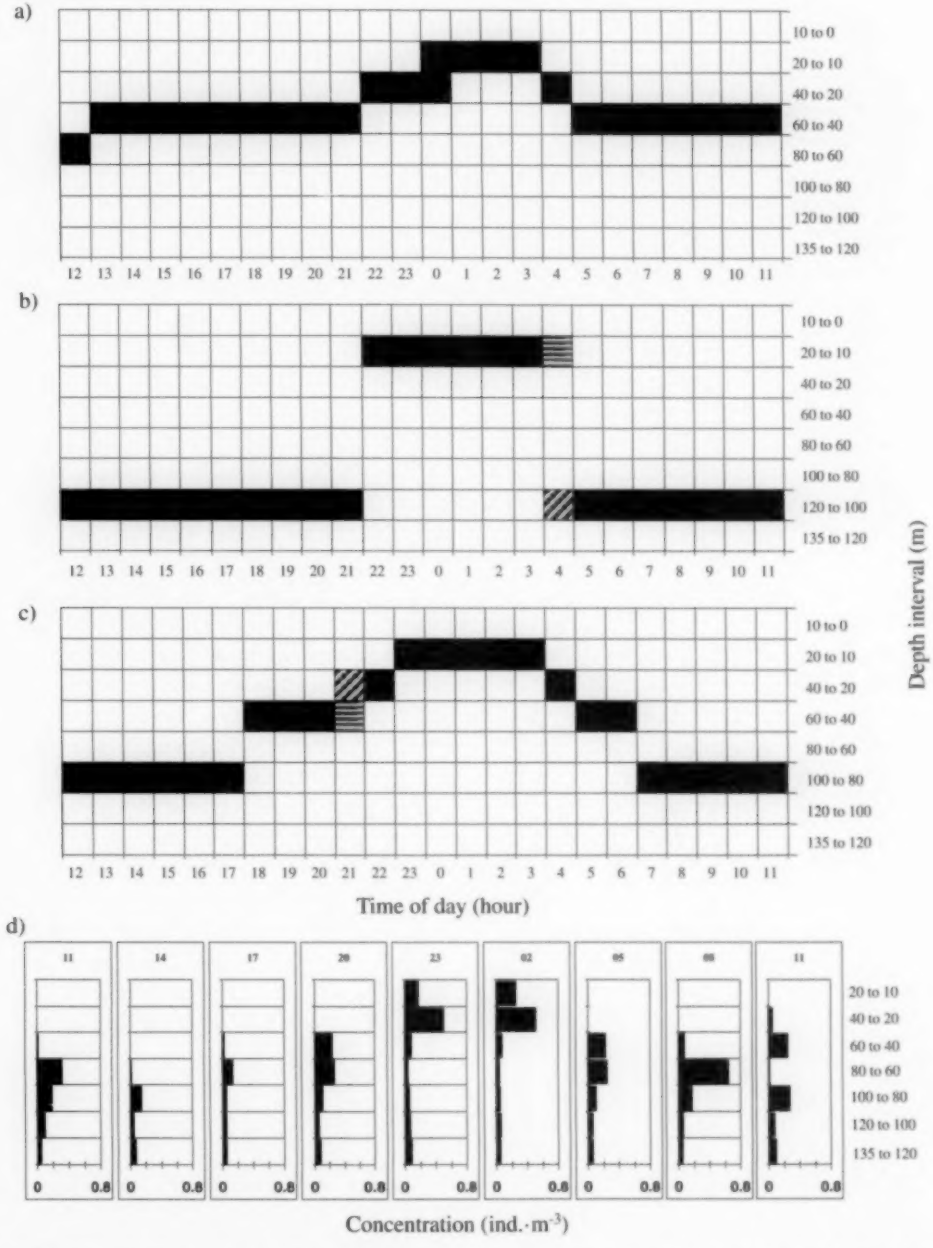
Fig. 4. Optimal time allocation strategy for a krill in the Clyde Sea (*a*) allowed to feed continuously over a 24-h period (fish density = 0.01·m^{-3}), (*b*) when fish density is 0.0001·m^{-3} (continuous feeding over 24 h), and (*c*) constrained from feeding during the daytime (fish density = 0.01·m^{-3}) (time allocation: horizontally hatched bars, >0 to 30 min; diagonally hatched bars, 30 min to <1 h; solid bars, 1 h). (*d*) Net-catch concentrations (MOCNESS, 1 m^2) of northern krill in the Clyde Sea between 4 and 5 July 1996 (local time of catch indicated at the top of each graph).



Cuzin-Roudy (1996) in the Ligurian Sea. The model was run with the density of predators increased and decreased by two orders of magnitude to investigate the effect of varying predator numbers on model predictions. When predator density was increased, the time allocation strategy remained the same in both the Clyde Sea and the Kattegat, although E increased to 0.10·day^{-1} in the Clyde Sea and to 0.89·day^{-1} in the Kattegat. This showed that when predator densities rise above 0.01 individual·m^{-3} in the Clyde Sea and 0.01 individual·m^{-3} in the Kattegat, the relative difference in risk between depth intervals remains approximately the same. Therefore, the model predicts that vertical migration behaviour does not

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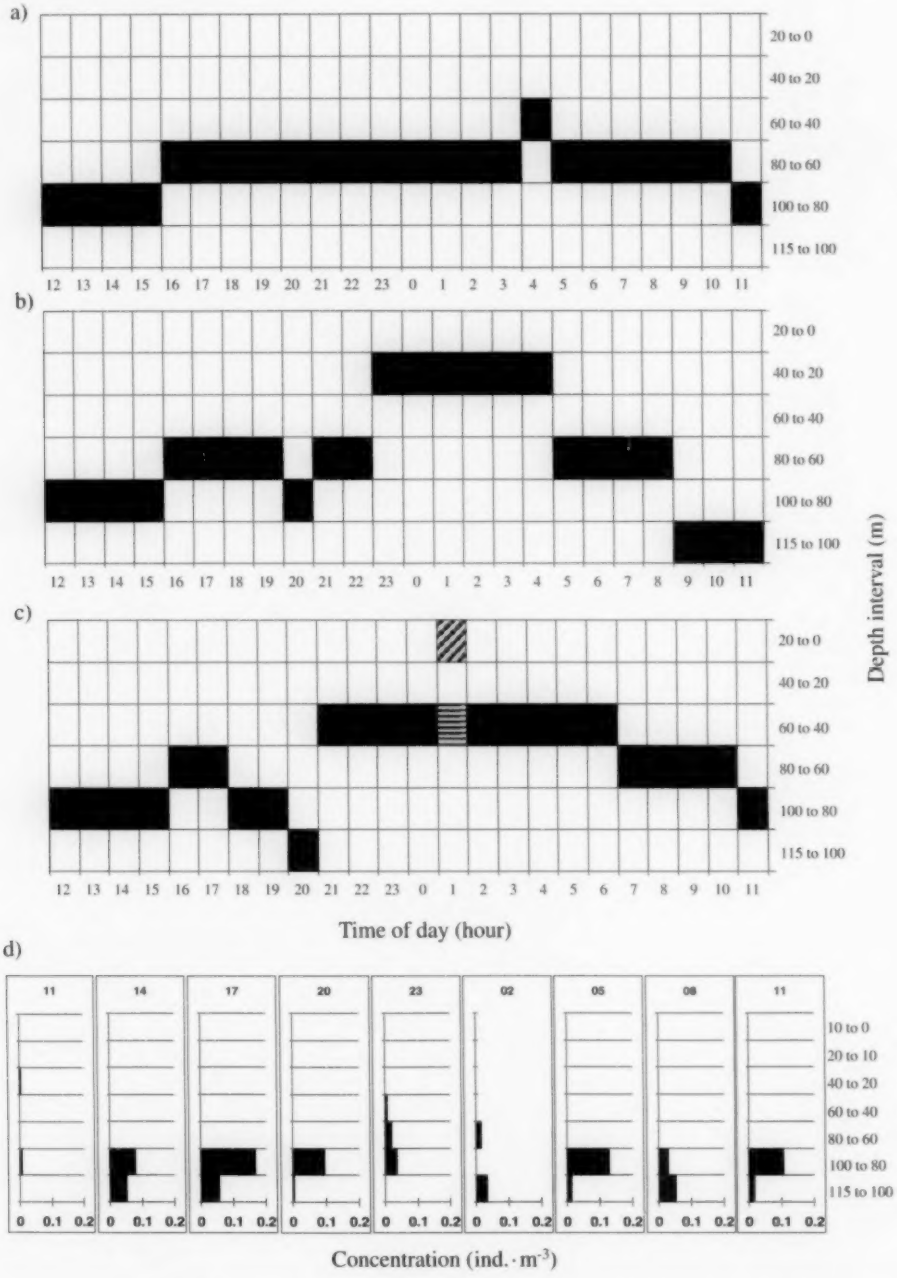
Fig. 5. Optimal time allocation strategy for a krill over a 24-h period in the Kattegat (*a*) allowed to feed continuously (fish density = $0.001 \cdot m^{-3}$), (*b*) when fish density is $0.00001 \cdot m^{-3}$ (continuous feeding for 24 h), (*c*) constrained from feeding during the daytime (fish density = $0.001 \cdot m^{-3}$) (time allocation: horizontally hatched bars, >0 to 30 min; diagonally hatched bars, 30 min to <1 h; solid bars, 1 h). (*d*) Net-catch concentrations (MOCNESS, 1 m^2) of northern krill in the Kattegat between 18 and 19 July 1996 (local time of catch indicated at the top of each graph).



change when there is a large influx of visual predators. When the predator density was decreased, the time allocation strategy did change such that the krill increased their time spent in the low risk, low energy gain environments and also in the high risk, high energy gain environments. For the Clyde Sea, this meant residence in the lowermost (low energy gain) depth intervals during daytime and the uppermost (high energy gain) depth intervals during night

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Table 4. Contribution to net energy gained (H_t') from copepod and phytoplankton ingestion, the loss to respiration, and the expected mortality rate (E) as a proportion of the population resulting from following the optimal time allocation strategy in the Clyde Sea and the Kattegat where feeding was continuous over 24 h and where feeding was constrained during daytime (fish density = 0.01·m^{-3} in the Clyde Sea and 0.001·m^{-3} in the Kattegat).

	H_t' (J·day^{-1})	E	Energy from copepods (J·day^{-1})	% of total body energy	Energy from phytoplankton (J·day^{-1})	% of total body energy	Energy for respiration (J·day^{-1})	% of total body energy
Continuous feeding								
Clyde Sea	14.000	0.000994	27.841	1.273	15.134	0.692	28.975	1.325
Kattegat	19.416	0.009082	33.641	1.539	0.076	0.003	14.301	0.654
Constrained feeding								
Clyde Sea	14.000	0.001492	23.890	1.093	19.329	0.884	29.219	1.336
Kattegat	7.050	0.013175	21.983	1.005	0.106	0.005	15.039	0.688

(Fig. 4*b*). For the Kattegat, low-gain environments occur in the midpart of the water column, while high gain occurs in both the deep and surface layers. Therefore, the pattern here was movement from midwater to the surface around midnight and from midwater to deep around midmorning (Fig. 6*b*).

Overall, the model predicts that when fish density is high, the optimal strategy is to maximise time in medium risk, medium energy return environments. In low fish density situations, greater time may be spent in the higher risk environments where most of the day's energy requirements may be obtained, thus allowing the krill to spend the majority of the day in very low risk, low energy return environments.

Temperature

The effect of temperature stratification was investigated by making the water column a uniform temperature. Two runs were carried out, one using the maximum temperature observed and the other using the minimum temperature. There was very little difference in the resulting time allocation strategies for either temperature that was used in both the Clyde Sea and the Kattegat. Temperature was therefore not considered particularly important in influencing predicted migration patterns.

Krill feeding strategy

The model assumed that krill were able to feed continuously over the 24-h period. A further constraint was added so that krill could only feed during "nighttime" (18:00–06:00). In both the Clyde Sea and the Kattegat, the resulting time allocation strategies produced higher values for E than for the original model runs (Table 4). This is to be predicted, since the krill must increase time in the higher energy gain, higher risk environments, as there is a shorter time available in which to feed. In the Clyde Sea, the krill move above 40 m by 22:00 and then occupy the 20- to 10-m depth interval for 5 h. During daytime, when the model constrains the krill from feeding, their optimal strategy is to occupy the lowest risk environment between 100 and 80 m (Fig. 4*c*). For the Kattegat, the optimal strategy is to occupy the 60- to 40-m depth layer during the period when the model allows krill feeding and then to spend an hour in the high risk, high energy gain environment at the surface and an hour in the deepest depth interval. Periods when feeding is not allowed are spent between 60 and 100 m (Fig. 6*c*).

Discussion

A MOCNESS net was used over a 30-h period in the Clyde Sea and the Kattegat to investigate the vertical migration behaviour of northern krill (see Tarling et al. 1998*b*). The results of the net-catch study are presented in Figs. 4*d* and 6*d*. For the Clyde Sea, the original run of the model predicted a daytime distribution that was between 20 and 40 m higher than found in the field observations. Nevertheless, both the predicted timing of the nighttime migration into and out of the upper layers and the upper depth limit of migration closely matched observations. The predictions of the model run with the added constraint on feeding during daytime were closer to the observed daytime depth of the krill population. The predicted timing of upward migration and the upper migration limit were also similar to observations. For the Kattegat, there was little predicted vertical movement during nighttime in the original run of the model, unlike that inferred from the net-catch data (see Tarling et al. 1998*b*). However, the predicted daytime depth of below 80 m was similar to observations. As with the Clyde Sea, the constraint on feeding during daytime produced model predictions that were closer to field observations. In this instance, upward migration during nighttime was predicted, although the predicted daytime depth was occasionally one depth interval higher than observed.

The comparison of model predictions in the Clyde Sea and the Kattegat illustrates that the model is successful in predicting DVM in two localities with contrasting distributions of food and predation risk. The model would therefore seem to be a good representation of the true processes controlling the vertical migration behaviour of northern krill. This assumes that krill in the Clyde Sea and the Kattegat have a common response to patterns of light levels (determining vulnerability to predators) and distributions of food. Furthermore, the sensitivity of model predictions to variations in predator density and feeding regime show that it is food and predation risk that drive the predicted DVM patterns. The lack of sensitivity to temperature effects on metabolic costs shows that the model predicts this to be a relatively minor influence on DVM patterns.

Feeding

Field observations of northern krill show a clear pattern of DVM in both the Clyde Sea and the Kattegat. The Clyde Sea has relatively weak thermal stratification and high concentra-

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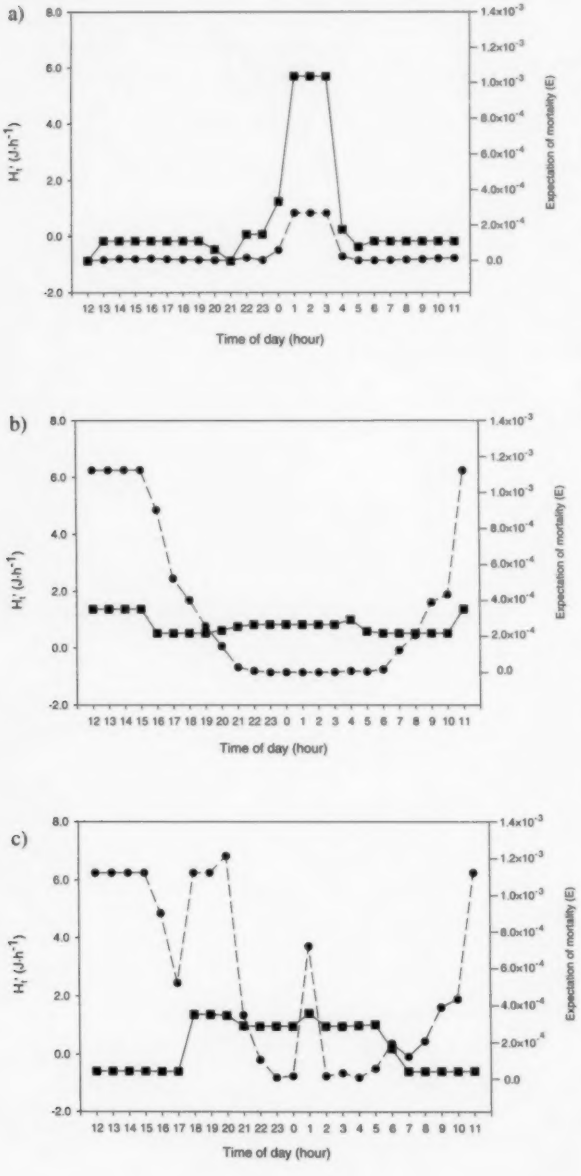
Fig. 6. Rate of energy gain and expected mortality for a krill following the optimal time allocation strategy over a 24-h period in (*a*) the Clyde Sea when allowed to feed continuously (fish density = $0.01 \cdot m^{-3}$), (*b*) the Kattegat when allowed to feed continuously (fish density = $0.001 \cdot m^{-3}$), and (*c*) the Kattegat when constrained from feeding during the daytime (fish density = $0.001 \cdot m^{-3}$).



tions of food items (both phytoplankton and copepods) in the surface layers, and consequently relatively high light attenuation near the surface. This contrasts with deep trench habitats in the Kattegat, where there is a strong thermocline (10°C gradient) and a relatively even distribution of food items (principally copepods) through the water column, with less attenuation near the surface. As a result of these differences, the model predicts more pronounced DVM in the Clyde Sea than in the Kattegat. At greater depths in the Clyde Sea, food is comparatively less abundant than in the Kattegat, yet because of the greater light attenuation, predation risk is also reduced relative to the Kattegat. To achieve the same level of food intake as in the Kattegat, the krill in the Clyde Sea must ascend to nearer the surface at night. Likewise, the krill in the Kattegat must go deeper by day to minimise predation risk. Because prey is distributed throughout the water column in the Kattegat, these animals need not ascend so much as in the Clyde Sea. The model successfully reproduces these intersite differences in DVM as a direct result of the difference in prey and light attenuation.

One interesting further feature was that model predictions for DVM were closer to field observations in both the Clyde Sea and the Kattegat when a constraint of feeding during the daytime was imposed. The ability of the krill in the Kattegat to feed on a rich community of copepods during the daytime results in a model predicting only a weak vertical migration into the upper layers at night. However, with the added feeding constraint, a more pronounced migration is predicted, closer to the patterns observed in the field. The laboratory experiments of Båmstedt and Karlson (1998) indicated that northern krill showed no diel rhythm in feeding activity, and field data from Onsrud and Kaartvedt (1998) indicated that northern krill fed on copepods day and night. This is in contrast with the results of the PEP programme (Lass 1998; J. Matthews, unpublished data) where it was found that the stomach contents of northern krill in the deep layers of the Kattegat during daytime primarily contained a copepod species (*Temora longicornis*) that was exclusively found in the surface layers. This suggests that the majority of feeding activity occurred during the nighttime period when the krill moved into the upper layers. The fact that model predictions were closer to observed patterns when krill were constrained from feeding during daytime supports the hypothesis that krill may exhibit a diel rhythm in feeding activity in certain environments. What is also evident from the model is that undertaking a diel feeding rhythm also results in a greater expectation of mortality, as the animal enters riskier environments to obtain a greater feeding rate in the limited time available. Therefore, undertaking a diel feeding rhythm may indicate that there are extra costs in feeding in the deeper layers during daytime that have not been considered here. For instance, feeding makes the foraging zooplankton less transparent (see Giske et al. 1994), which may present greater risks in the dim light levels in the deep during daytime than at the surface during the night. Also, the deeper layers contained a greater proportion of *Calanus* (Lass 1998; J. Matthews, unpulished data), which are larger and are more likely to have a stronger escape response than the smaller *Temora* at the surface.

Predation levels

Unlike the Clyde Sea, where predation risk is highest during the nighttime, in the Kattegat, predation risk is highest during the day, even when the feeding constraint is added. This highlights the fact that the Kattegat is a riskier environment than the Clyde Sea for two reasons. Firstly, the attenu-

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ation coefficient is lower, resulting in greater light penetration and greater risk of visual predation at the middle of the water column. Secondly, the water column is shallower, so a movement to depth to avoid visual predation results in the animals being near bottom and close to tactile bottom-dwelling predators. Therefore, whereas the Clyde Sea krill may take refuge during the daytime from predation in the middle of the water column where there is little visual or tactile predation, krill in the Kattegat must trade-off the relative risk of one predation type with another. During the daytime, the risk from bottom-dwelling predators is much less than that from visual predators and a deep daytime distribution is preferable.

Mortality rates for zooplankton are inherently difficult to estimate (McGurk 1986), and although the presence or absence of major predators may be indicated by pelagic trawls and multifrequency acoustics (Kaartvedt et al. 1996), gaining estimates of fish predator density is beyond the scope of current oceanographic study. Sensitivity analyses were used to predict the effect of altering fish densities over two orders of magnitude on the DVM pattern. Although estimating predation levels is a weakness in trade-off models, the present model design places much greater reliance on estimating the relative rather than the absolute risk of predation throughout the water column. In this sense, therefore, the accuracy of the model predictions depend much more on the foraging ability of the fish predator under light levels that change according to depth and time of day, which are aspects that have been modelled and validated to an accurate degree (Fiksen et al. 1998 and references therein). The biggest improvement to the predation aspect of the model will be in determining the risk from less visually dependent bottom-dwelling predators such as cod in relation to their visual pelagic counterparts.

What has been presented is a framework that is able to simulate migration patterns based on a set of forcing functions either obtained from the literature or measured directly from field sampling campaigns. Further data sets will no doubt improve the functions that are used so that real values for parameters are represented more accurately in simulations. It is also necessary that certain important assumptions in this approach, such as the freedom of movement between any depth interval and the lack of any added metabolic costs to vertical migration, be examined in greater detail. However, the power of this approach is in allowing the modeller to compare and contrast different DVM strategies where only relative vertical profiles of mortality risk and metabolic gain are reliable.

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Molecular phylogenetics of circumglobal *Euphausia* species (Euphausiacea: Crustacea)

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Abstract: The speciation history of members of the krill genus *Euphausia* with continuous circumglobal distributions was investigated by phylogenetic and molecular clock analyses of their mitochondrial DNA. Molecular clock estimates for divergence times of Antarctic and sub-Antarctic species of *Euphausia* of ~15 million years ago were fairly close to the time of formation of the Antarctic Convergence, consistent with their vicariant speciation. However, the confidence limits quantified for these time estimates were large at ~11 million and ~25 million years. A divergence time of between ~10 million years for *Euphausia triacantha* and *Euphausia longirostris* suggested that migration across oceanographic fronts like the Antarctic Convergence may also lead to speciation in krill. Genetic differentiation between *Euphausia vallentini* and *Euphausia lucens* was found to be relatively minor and occurred between 0.76 million and 1.65 million years ago. These species have overlapping ranges, suggesting that there is potential for sympatric genetic differentiation in krill.

Résumé : L'histoire de la spéciation des espèces de krill du genre *Euphausia* à répartition continue circumglobale a pu être étudiée par analyse phylogénétique et par l'analyse de l'horloge moléculaire de leur ADN mitochondrial. Les estimations obtenues à l'aide de l'horloge moléculaire font remonter à ~15 millions d'années la divergence entre les espèces antarctiques et subantarctiques d'*Euphausia*, ce qui correspond d'assez près à la période de la formation de la Convergence antarctique et est compatible avec leur spéciation vicariante. Cependant, les intervalles de confiance associés à ces estimations de temps sont grands, allant de ~11 à ~25 millions d'années. La divergence entre *Euphausia tricantha* et *Euphausia longirostris* date de ~10 millions d'années; il se peut donc qu'une migration à travers des fronts océaniques, tels que la Convergence antarctique, puisse aussi mener à la spéciation chez le krill. La différentiation génétique entre *Euphausia vallentini* et *Euphausia lucens* s'est avérée relativement faible et s'est produite il y a 0,76 – 1,65 millions d'années. Ces espèces possèdent des répartitions géographiques qui se chevauchent, ce qui indique qu'il est possible qu'il y ait de la différentiation génétique sympatrique chez le krill.

[Traduit par la Rédaction]

Introduction

Krill (order Euphausiacea) are some of the most abundant animals in the pelagic marine environment. The genus *Euphausia* is the most species rich of the Euphausiacea, accounting for 31 of the 85 known species (Baker et al. 1990). It contains two of the most abundant and economically important krill species, *E. superba* and *E. pacifica*. *Euphausia pacifica* is one of the most northerly representatives of the genus and is present over a large area of the northern Pacific. At the southern end of the range of *Euphausia*, the Antarctic krill *E. superba* is one of the world's most abundant animals with an enormous biomass and great significance in the Southern Ocean ecosystem (Mauchline and Fisher 1969; Nicol and Endo 1999).

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Euphausia contains nine species with continuous circumglobal distributions similar to that of *E. superba* (Mauchline and Fisher 1969). The distributions of seven of these circumglobal species and three other euphausiids, *E. pacifica*, *Meganyctiphanes norvegica*, and *Nyctiphanes australis*, are shown in Fig. 1. The distribution of euphausiids is thought to be delimited by water temperatures (Mauchline and Fisher 1969; Van der Spoel and Heyman 1983) and ocean currents (Van der Spoel and Heyman 1983; Patarnello et al. 1996). Furthermore, the present distribution of *Euphausia* must be related to past speciation events.

The division of higher taxa into morphological species is often the clearest and most easily detectable form of genetic differentiation. The presence of fixed phenotypic differences between species in the same genus allows simple allocation of individuals to different groups that are assumed to not interbreed. The latitudinal limits on distribution of the circumglobal species of *Euphausia* are strongly suggestive of gene flow occurring far faster longitudinally than latitudinally in southern waters.

The factors leading to genetic differentiation in the pelagic environment are poorly understood (Knowlton 1993; Palumbi 1994). Allopatric differentiation requires barriers to dispersal and these are not obvious in the freely circulating southern waters inhabited by the circumglobal species of *Euphausia* in this study. The sudden changes in water temperature and current direction at oceanic fronts are the most

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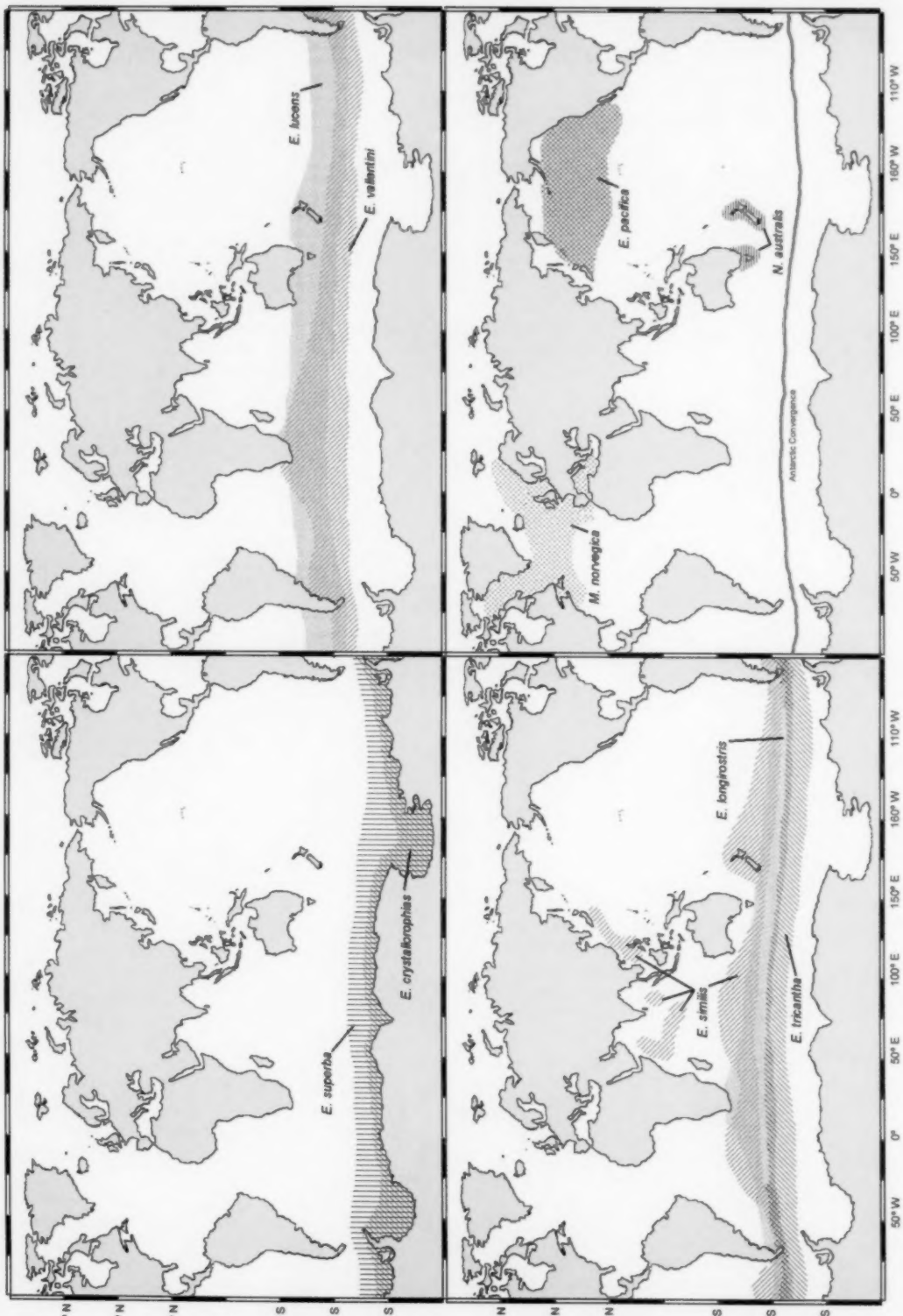

Fig. 1. Approximate horizontal distributions of krill species included in this study. Distributions are taken from Mauchline and Fisher (1969) and Van der Spoel and Heyman (1983).

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likely barriers to gene flow here (Schneppenheim and MacDonald 1984; Fevolden 1988; Patarnello et al. 1996). Even if these barriers are not complete, they may allow genetic differences on either side of the barrier to accumulate until a hybrid zone forms between the separate populations, which is often a precursor to parapatric speciation (Ridley 1996). The pelagic environment is also a potential location for sympatric differentiation (Knowlton 1993; Palumbi 1994). Evidence that this occurs in a range of other pelagic marine taxa comes from the identification of sibling species by genetic and morphological studies (Knowlton 1993; Bernard and Goswami 1997; Bucklin et al. 1998).

In this study, we explore evolutionary relationships between circumglobal species of *Euphausia* by phylogenetic analysis of mitochondrial large-subunit ribosomal DNA (16S rDNA) and cytochrome oxidase subunit I (COI) DNA sequences. There have been no thorough phylogenetic studies of relationships within this genus based on morphology, although the genus has been divided into four "groups" on the basis of general appearance. Of the species that we studied, *E. superba*, *E. crystallorophias*, *E. vallentini*, *E. lucens*, *E. similis*, and *E. pacifica* belong to group B, while *E. longirostris* and *E. triacantha* belong to group D (Hansen 1911; Mauchline and Fisher 1969). The only previous phylogenetic study of *Euphausia* species by Patarnello et al. (1996) used 16S rDNA data. We expand this data set with data from another mitochondrial region and from extra taxa. The relationships between these species and the times that they diverged from each other are estimated. This speciation history gives us information on the processes that have led to genetic differentiation in these krill.

Materials and methods

Laboratory procedures

Samples of eight *Euphausia* species (*E. crystallorophias*, *E. superba*, *E. lucens*, *E. triacantha*, *E. similis*, *E. longirostris*, *E. vallentini*, and *E. pacifica*) and two other krill species (*M. norvegica* and *N. australis*) were collected from a range of sites around the world. DNA was extracted from tissue preserved in 70–80% ethanol with a modified Chelex rapid-boiling procedure (Walsh et al. 1991). Approximately 0.5 mg of abdominal muscle was placed in a 1.5-mL microcentrifuge tube containing 200 µL of 6% Chelex® 100 resin (Bio-Rad) in 50 mM Tris, pH 8.0, and 0.5 mM EDTA. The tube was heated at 100°C for 8 min and then centrifuged at 20 000 × *g* for 10 min. The resulting supernatant was removed to a new 1.5-mL centrifuge tube and later used as a template for polymerase chain reaction (PCR) amplifications.

Portions of two mitochondrial genes were amplified by PCR from single individuals of each species using "universal" primers. Approximately 530 base pairs of the 16S rDNA were amplified using the primers 16Sar (5′-CGCCTGTTTATCAAAAACAT-3′) and 16Sbr (5′-CCGGTCTGAACTCAGATCACGT-3′) (Palumbi et al. 1991). This region is considered generally appropriate for studies of Cenozoic speciation events (Hillis and Dixon 1991) and has been used commonly with phylogeny of Crustacea (Cunningham et al. 1992; Schubart et al. 1998). About 720 base pairs of COI were amplified using the primers LCO (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer et al. 1994). The COI region evolves slightly faster overall than the 16S region because it has sites where synonymous mutations may occur (Schubart et al. 1998) but has also been used for phylogeny in recent Crustacea (Ovenden et al. 1997; Schubart et al. 1998).

Fifty-microlitre PCR reactions contained 0.1% Triton X-100, 50 mM KCl, 10 mM Tris–HCl pH 9.0, 2.5 mM $MgCl_2$, 0.25 mM of each dNTP, two units of *Taq* DNA polymerase (Promega), 10 pmol of each primer, and 5 µL of the Chelex-extracted DNA as a template. Cycle conditions were 94°C for 30 s and then 40 cycles of 94°C for 30 s, 52°C for 1 min, and 72°C for 1 min 30 s followed by 72°C for 6 min. Contamination from exogenous DNA was avoided by performing all manipulations in a laminar flow cabinet and using aerosol-resistant pipette tips. A DNA-free negative control was included in every batch of PCR reactions. The batch was discarded if the negative control showed an amplification product.

Completed PCR reactions were electrophoresed through a 1% agarose, 0.5 µg ethidium bromide·mL^{-1} gel in 1× Tris actate EDTA (TAE) buffer at 5 V·cm^{-1}. The DNA band formed by the PCR product was excised from the gel under 300-nm illumination. DNA was extracted from the agarose using a Quiaex II gel extraction kit (Quiagen). Final PCR product DNA concentration was measured using a TKO-400 fluorometer (Hoefer Scientific Instruments).

Both strands of the 16S rDNA and COI PCR products from each species were sequenced using BigDye terminator sequencing reactions (ABI) in which 5 µM of each primer was used to prime amplification from 30–40 ng of PCR product. The resulting sequencing reactions were analyzed on an ABI 377 automated DNA sequencer.

Analysis of nucleotide sequence data

Sequence data for both strands of each PCR product were analyzed and aligned using Sequence Navigator (ABI) software. Sequence data for krill were deposited in GenBank (accession Nos. AF177176–AF177191). 16S rDNA data for *Gonodactylus graphurus* were given accession No. AF133678. The 16S rDNA sequences for *E. superba* was taken from GenBank record M98483. Data for *E. crystallorophias*, *E. vallentini*, and *M. norvegica* were taken from records Z73806, Z73804, and Z73803, respectively, which were deposited by Patarnello et al. (1996).

The 16S rDNA and COI sequences were aligned separately using ClustalX (Thompson et al. 1997). Alignments were executed under the settings of 15 for "gap opening" and 5 for "gap extension," with transitions weighted at 0.5 and the alignment of sequences more than 40% divergent delayed until the other sequences were aligned.

Phylogenetic analyses

ClustalX alignment files were imported into PAUP* 4.0b2 (Swofford 1998) for phylogenetic analysis. The 16S rDNA and COI alignments were combined into a single file. Gapped positions created by ClustalX sequence alignment were excluded from the analyses to help ensure that characters compared were orthologous.

Minimum evolution (Rzhetsky and Nei 1992) searches were conducted with the HKY85 nucleotide evolution model (Hasegawa et al. 1985) to allow for unequal rates of transitions and transversions and to accommodate the unequal equilibrium base frequencies of this AT-rich data set. Discrete gamma correction (Γ) for among-site rate heterogeneity (Yang 1994) with eight rate categories is added to accommodate rate variation within and between the COI and 16S rDNA regions. This correction is also worth including, as among-site rate variation has been shown to strongly affect estimates of divergence dates from molecular data (Yang 1996). The α parameter of the discrete Γ distribution for the combined 16S rDNA and COI data set was estimated to be 0.170 when optimized along with the transition to transversion ratio and equilibrium base frequencies of the data set by maximum likelihood on a tree generated under the HKY85 model without Γ correction. The equilib-

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rium base frequencies were estimated to be πA 0.329, πC 0.142, πG 0.151, and πT 0.378 and the transition to transversion ratio to be 2.156. These estimates demonstrated skewed base frequency, unequal transition to transversion ratio, and extensive among-site rate variation. The application of the HKY85 + Γ model was therefore appropriate for the combined 16S rDNA and COI data set.

Estimates for these parameters were also made for the COI and 16S rDNA data separately. The 16S rDNA parameters were α = 0.144, πA 0.374, πC 0.106, πG 0.158, πT 0.362, transition to transversion ratio 1.641, and the COI parameters were α = 0.190, πA 0.301, πC 0.162, πG 0.148, πT 0.387, transition to transversion ratio 2.621. These estimates were very close to those made for the combined data set, which confirmed the applicability of a single set of parameters to the combined data set in minimum evolution analysis. To assess whether the data from the two mitochondrial regions supported the same phylogeny, a partition homogeneity test (Farris et al. 1995) with 2000 replicates was applied. The *P* value of $0.5 > P > 0.2$ allowed the null hypothesis of consistent phylogenetic signal between the COI and 16S rDNA partitions of the combined data set to be accepted.

In maximum parsimony (Swofford 1998) analysis of the combined data set, transversions in the 16S rDNA region were weighted as twice as significant as transitions to allow for the greater likelihood of transitional mutations indicated by the 1.641 transition to transversion ratio estimated for this region. Transversions in the COI region were given three times the weight of transitions, based on a transition to transversion estimate of 2.621 for this region. These weightings were the nearest whole number ratio to the transition to transversion ratio estimated by maximum likelihood, as weightings implemented with step matrices must be integers.

Trees were found by heuristic searches. Bootstrap pseudoreplication (Felsenstein 1985) was used to estimate statistical confidence in nodes, with each tree resampled 2000 times for reliable estimation of bootstrap support (Hedges 1992).

Molecular clock test

A likelihood ratio test (Felsenstein 1988; Huelsenbeck and Crandall 1997) was used to test whether variation in 16S rDNA evolutionary rate within the circumglobal *Euphausia* was significant enough to reject a null hypothesis of stochastically constant evolutionary rate. The 16S rDNA sequences were taken from the same alignment used in the phylogenetic analyses. Maximum likelihood trees were constructed with PAUP, estimating all the free parameters of the HKY85 + Γ sequence evolution model with a molecular clock enforced (–ln likelihood 962.001) and without an enforced clock (–ln likelihood 966.464). Twice the difference in the –ln likelihoods of these trees ($\delta = 8.926$) was used as a test statistic for a χ^2 distribution with 5 degrees of freedom (*n* taxa – 2). The *P* value of $0.2 > P > 0.1$ obtained allowed the null hypothesis of clock-like 16S rDNA evolution in these euphausiids to be accepted. This meant that a single 16S rDNA evolutionary rate could be applied to the circumglobal *Euphausia* to estimate divergence times for these species.

Molecular clock calibration

It was not possible to directly calibrate the 16S rDNA molecular clock of *Euphausia*, as the speciation events under examination could not be correlated with biogeographic events having known dates. Estimates of the evolutionary rate for the 16S rDNA in krill were made by referring to rates of 16S rDNA sequence change in grapsid crabs (data from Schubart et al. 1998). Closely related grapsids occur on either side of the Isthmus of Panama, which formed 3.1 million years ago (mya), separating several species pairs (Knowlton 1993; Schubart et al. 1998). Pairwise 16S rDNA genetic distances (HKY85 + Γ model) for these species pairs were calculated. The α shape parameter of the Γ distribution was estimated on an HKY85 tree along with the other free parameters of this model, transition to transversion ratio and equilibrium base frequencies. A linear regression was generated from the genetic distances (independent variable) against 3.1 million years (dependent variable) and zero genetic distance at zero time. This regression was used to estimate (Hillis et al. 1996) the 16S rDNA evolutionary rate in grapsids, which was 0.640 ± 0.063% SE sequence change per million years.

To compare the grapsid and krill 16S rDNA evolutionary rates, a minimum evolution tree relating the krill species in this study, the 11 non-Jamaican grapsids from Schubart et al. (1998), and their common outgroup *G. graphurus* (Malacostraca: Stomatopoda) was constructed from their 16S rDNA sequences. Genetic distance (HKY85 + Γ model, eight rate categories) was estimated for all species pairs. The mean genetic distances separating the last common ancestor (LCA) of krill and grapsids from each of these groups were calculated using the method of Sarich and Wilson (1973). Division of the krill LCA mean of 0.261 ± 0.034 SE by the grapsid LCA mean of 0.241 ± 0.027 SE gave an estimate of the rate of krill 16S rDNA evolution to be 1.086 ± 0.187 SE times the rate of grapsid 16S rDNA evolution in the time since the two groups diverged from their common ancestor. Multiplying these relative values by the absolute rate of 16S rDNA evolution for grapsids of 0.640 ± 0.063% SE gives a rate estimate of 0.695 ± 0.123% SE sequence change per million years for krill 16S rDNA.

Ninety-five percent confidence limits on the rate estimate were calculated by multiplying the SE of the 16S rDNA rate estimate for krill by the critical value of 2.086 for Student's t $\alpha(2)$ 0.05 at 20 degrees of freedom (*n* taxa compared – 1). This set lower and upper 95% confidence limits on 16S rDNA evolutionary rate for krill at 0.438 and 0.951% sequence change per million years, respectively.

Results

Alignments

Alignment of the COI data in ClustalX produced a 603-base alignment with no gaps that was congruent with an alignment of the protein translation of the sequences. Of the 206 variable sites, 197 resulted from synonymous mutations. The 16S rDNA data alignment was 450 characters long and had 22 gapped positions, which were excluded from phylogenetic analyses.

Phylogenetic analyses

The phylogenies generated by minimum evolution and maximum parsimony optimality criteria for the relationships between eight species of *Euphausia* based on their 16S rDNA and COI sequences are shown in Fig. 2. The minimum evolution tree had a minimum evolution score of 1.018. The maximum parsimony tree based on 212 parsimony informative characters was 1001 steps long with weighting (566 steps without) and had a consistency index of 0.670 and a retention index of 0.546.

The outgroup is *N. australis* because an initial phylogeny containing *N. australis* and *M. norvegica* and polarized using the distantly related *G. graphurus* suggested that *N. australis* was more closely related to the ingroup than to *M. norvegica*. Outgrouping with *N. australis* would therefore cause less misalignment between the ingroup taxa, and there would be less homoplastic change between it and the ingroup. Outgrouping with *M. norvegica* or *G. graphurus* still produced trees with identical topology, although bootstrap support for several nodes was slightly reduced.

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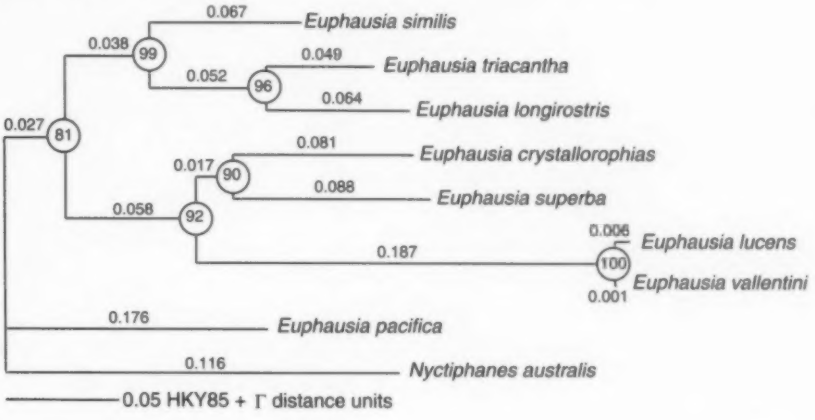
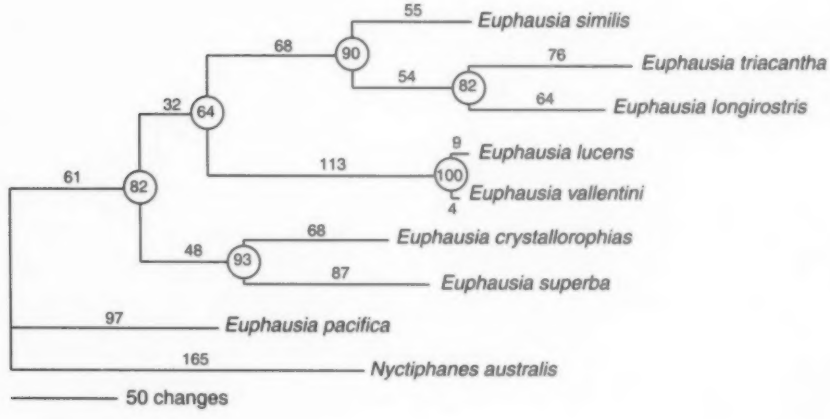
Fig. 2. Minimum evolution and maximum parsimony phenograms showing relationships among seven species of circumglobal *Euphausia* and *E. pacifica*. *Nyctiphanes australis* is the outgroup. Branch lengths are shown above each branch. Bootstrap support values for nodes are given in a circle on each node.



Minimum evolution



Maximum parsimony

Both trees give strong support for the species pairs *E. crystallorophias* – *E. superba*, *E. vallentini* – *E. lucens*, and *E. longirostris* – *E. triacantha*. There is also strong support for *E. similis* being closely related to *E. triacantha* and *E. longirostris*. Support is also given for separation of the southern hemisphere *Euphausia* from the northern hemisphere *Euphausia pacifica*.

There is some difference in topology between the trees generated by the two analysis methods at the deeper nodes within *Euphausia*. The minimum evolution tree suggests that *E. superba* and *E. crystallorophias* group with *E. vallentini* and *E. lucens*. The maximum parsimony tree gives very weak support for *E. vallentini* and *E. lucens* being more closely related to *E. similis*, *E. longirostris*, and *E. triacantha*. This inconsistency cannot be resolved without gathering more data but does not affect the conclusions of this study.

Estimation of divergence times

The rate of 16S rDNA evolution in the krill taxa examined was shown to be homogeneous by a likelihood ratio test. The 16S rDNA molecular clock for these krill was estimated to evolve at 0.695 ± 0.123% SE sequence change per million years by comparison with a known rate in grapsid crabs. Speciation dates for *Euphausia* estimated with the krill 16S rDNA molecular clock are shown in Table 1. Evolutionary events that might correlate with these estimated divergence times are shown.

Discussion

Krill have some of the largest populations known for sexually reproducing metazoans. At less than 1 g each, *E. superba* numbers as many as 5×10^{14} individuals, given biomass es-

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Table 1. Estimations of divergence times in millions of years for circumglobal species of *Euphausia*.

Event	Species 1	Species 2	16S rDNA HKY85 + Γ genetic distance	Lower 95% limit	Estimate	Upper 95% limit
Possible sympatric speciation	*E. vallentini*	*E. lucens*	0.007238	0.76	1.04	1.65
Possible allopatric speciation by migration across Antarctic Convergence	*E. longirostris*	*E. tricantha*	0.066178	6.96	9.53	15.09
	E. tricantha	*E. similis*	0.089619	9.43	12.90	20.44
Possible vicariant speciation of Antarctic and sub-Antarctic species	*E. superba*	*E. lucens*	0.115244	12.12	16.59	26.29
	E. superba	*E. vallentini*	0.110263	11.60	15.87	25.16
	E. crystallorophias	*E. vallentini*	0.099711	10.49	14.36	22.75
	E. crystallorophias	*E. lucens*	0.100236	10.54	14.43	22.87

Note: The estimates are based on an evolutionary rate estimate of 0.695% sequence change per million years and the 95% confidence intervals based on rates of 0.438 and 0.951%.

timates of up to 500×10^6 t (Nicol and Endo 1999). These large population sizes combined with a continuous distribution and high dispersal ability (Mauchline and Fisher 1969) mean that the isolation of subpopulations that might become differentiated through genetic drift is unlikely. All of the circumglobal euphausiids maintain a morphologically uniform population around the circumference of the earth. Allozyme studies indicate that there is no genetic subdivision of the *E. superba* population (Schneppenheim and MacDonald 1984; Kühl and Schneppenheim 1986; Fevolden 1988). There is, however, recent evidence of small mitochondrial DNA differences between *E. superba* populations near South Georgia and from the Weddell Sea, although differences between these sites and others in the Southern Ocean were not detected (Zane et al. 1998). Given these observations, how has speciation occurred in the southern *Euphausia*?

It would have been ideal to include all members of *Euphausia* for this study, but its global distribution and relative inaccessibility made this impractical. We can, however, deduce new information about evolution in *Euphausia* from the species that we did include. We can determine the nearest relatives of several krill species from among the species included in our phylogenies. *Euphausia vallentini* and *E. lucens* receive strong statistical support for their close relatedness and have an extensive range overlap. The estimate of divergence time for these two species is ~1 mya. The open ocean is a stable environment and we can be reasonably confident of circulation conditions being consistent since 2.5 mya, as indicated by microfossils of planktonic foraminifera (Murray 1995). This suggests that genetic differentiation between *E. vallentini* and *E. lucens* took place without the dispersal barriers provided by oceanographic fronts and that speciation was sympatric or perhaps parapatric. Another reasonable interpretation is that these are not separate species. The observation of Mauchline and Fisher (1969) that the diagnostic feature of *E. vallentini*, the shape of the antennular lappet, is variable, and the separation of *E. vallentini* from *E. lucens* on the basis of this feature in their key suggests that morphological differentiation between the two species is minor as well.

Euphausia superba and *E. crystallorophias* also appear to be closely related. The two species have an extensive range overlap now, but their divergence is estimated to have occurred ~5 mya and there is far less certainty of their ranges coinciding at that time, so it is not reasonable to speculate on their mode of speciation. The common ancestor of *E. superba* and *E. crystallorophias* may have been isolated from the common ancestor of *E. vallentini* and *E. lucens* by the formation of the Antarctic circumpolar current, as recognized by Patarnello et al. (1996). They used a different molecular clock calibration than ours that estimated this event at 19.5 mya, which correlates closely with the estimated time of formation of the Antarctic Convergence. Our more recent estimate of ~15 mya does not contradict this, given that our 95% confidence limits are between ~13 and ~26 mya. However, the quantification of these confidence limits, which are quite wide, shows that correlation of speciation events with reliably dated geographic events requires more data than are present in the 16S rDNA to reduce the error of the estimates.

Another species group to receive significant bootstrap support in our analysis is *E. triacantha* and *E. longirostris* as a pair and *E. similis* as a more distant relative. This observation is compatible with the division of *Euphausia* into its four groups by Hansen (1911) if we accept that group B is paraphyletic and group D, containing *E. longirostris* and *E. triacantha*, is derived from group B. *Euphausia triacantha* is found on either side of the Antarctic Convergence, and *E. longirostris* and *E. similis* are only found north of it. *Euphausia triacantha* is estimated to have diverged from the other two species at ~9.5 and ~13 mya. This indicates that colonization over the Antarctic Convergence is possible because it formed ~20 mya and that it may not provide an effective barrier to dispersal in *Euphausia*.

Allopatric speciation resulting from population subdivision is the best understood mechanism for causing the genetic differentiation that leads to speciation. It is probable that the formation of the Antarctic Convergence caused a reduction in latitudinal dispersal ability for the southernmost *Euphausia* species of the time and this led to the divergence of species north and south of the convergence, as previously recognized (Patarnello et al. 1996). However, *E. triacantha* is found on either side of the convergence now, and its divergence from a close relative only found north of the convergence was estimated to have occurred after the convergence formed. This indicates that for some *Euphausia*, genetic differentiation may result from migration across existing oceanographic fronts rather than from vicariance. There is also the possibility that sympatric speciation has occurred between

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E. vallentini and *E. lucens*. Further genetic investigation to determine whether these two morphological species are genetically distinct and whether the two morphotypes interbreed or not would be worthwhile.

Population genetics studies are another useful way to further investigate modes of genetic differentiation in krill, as they may uncover genetic differences between populations or even reveal cryptic species that subdivide the recognized morphological species (Knowlton 1993). This approach has been successful in identifying sympatric sibling species in other pelagic organisms such as marine copepods (Bucklin et al. 1998) and notothenoid fishes (Bernard and Goswami 1997). Recent studies using variable mitochondrial regions in krill have demonstrated genetic differentiation within *M. norvegica* (Bucklin et al. 1997) and *E. superba* (Zane et al. 1998) and show that genetic techniques may be useful for identifying species boundaries in krill.

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Is social aggregation in aquatic crustaceans a strategy to conserve energy?

D.A. Ritz

Abstract: Antarctic krill, *Euphausia superba*, is preeminently a gregarious animal. It lives for almost the whole of its existence from the late furcilia stage in aggregations. Despite this, laboratory study of schooling and swarming behaviour has been seriously neglected and critical emergent properties of group dynamics may have been overlooked. Using different-sized groups of gregarious mysids, I show that weight-specific oxygen uptake is reduced by about seven times when they form cohesive aggregations compared with when they are in uncohesive small groups. If this is true for *E. superba*, it casts doubt on all previous measurements of metabolic rate and suggests that estimates of the metabolic cost of swimming and perhaps feeding are much too high. The reason that groups conserve energy compared with isolates or small groups is hypothesised to be at least partly due to hydrodynamic processes, which serve to minimise sinking rates. Dye plumes revealed updrafts generated by mysid swarms, which could be exploited by individuals to reduce their sinking rate. These circulation patterns might also increase the efficiency of particle capture by aggregations. I propose that aggregation in aquatic crustaceans is a strategy to optimise energy expenditure and maximise food capture. Measuring behavioural and physiological rate processes in isolated animals will produce only artifacts.

Résumé : Le krill antarctique, *Euphausia superba*, est un animal éminemment grégaire, qui passe presque toute sa vie, à partir de la fin du stade furcilia, en grands rassemblements. Cependant, l'étude en laboratoire du comportement de regroupement en banc ou en essaim a été gravement négligée, et il est possible que certaines caractéristiques critiques de la dynamique des groupes soient méconnues. À partir de groupes de différentes tailles de mysidacés grégaires, je montre que l'absorption d'oxygène spécifique au poids est réduite de sept fois environ quand ces organismes forment des regroupements homogènes par rapport aux petits groupes non soudés. Si cela est vrai pour *E. superba*, on peut douter de la validité de toutes les mesures antérieures du métabolisme, et penser que les estimations du coût métabolique de la nage et peut-être même de l'alimentation sont beaucoup trop élevées. La raison pour laquelle les grands groupes conservent leur énergie par rapport aux individus isolés ou aux petits groupes pourrait se trouver au moins en partie dans les processus hydrodynamiques qui servent à réduire le taux d'enfoncement. Des panaches de teinture ont révélé l'existence de courants ascendants générés par les essaims de mysidacés, qui pourraient être exploités par les individus pour réduire leur taux d'enfoncement. Ces patrons de circulation pourraient aussi accroître l'efficacité du captage des particules par les rassemblements. Je pose que le regroupement chez les crustacés aquatiques est une stratégie visant à optimiser la dépense d'énergie et à maximiser le captage de la nourriture. La mesure des processus comportementaux et physiologiques chez les individus isolés ne peut produire que des artéfacts.

[Traduit par la Rédaction]

Introduction

Antarctic krill, *Euphausia superba*, is preeminently a social species, spending virtually the whole of its postfurcilial life in aggregations (Hamner et al. 1989). Close association with conspecifics has been postulated to deliver both costs and benefits to individuals of gregarious aquatic species (e.g., Ritz 1994, 1997). The greatest benefit is generally claimed to be protection from predation, mainly derived from group avoidance strategies and evasion and dilution factors once a successful attack is launched (e.g., O'Brien and Ritz 1988). Feeding benefits have been hypothesised and occasionally tested experimentally on a few gregarious species (Ritz 1997). Costs of feeding in groups are usually identified as competition, and results showing an optimum group size for capture success support this idea (Ritz 1997). Note though that Ritz's (1997) results showed that both sub-optimal and supra-optimal group sizes of suspension-feeding mysids captured food less successfully. Moreover, when threatened by a predator, mysids in small swarms captured significantly less food than those in large ones. Feeding can be traded for safety and large groups are advantageous (Ritz 1997). It is likely that these results are equally applicable to *E. superba*, but this has never been tested. Only Strand and Hamner (1990) and O'Brien (1989) described *E. superba* forming cohesive aggregations in laboratory tanks.

One benefit of aggregating that is often proposed but rarely tested is that it is a means of economising on energy expenditure (Hamner and Parrish 1997). The idea of the group as an energy-saving device is expressed in fish in the form of hydrodynamic benefits related to the exploitation of shed vortices from neighbours to facilitate forward swimming (Weihs 1975). Although this theory has a long history, predictions based on it have never been confirmed experimentally (e.g., Pitcher and Parrish 1993). Moreover, aggregation as an energy-saving strategy of gregarious aquatic invertebrates has never been directly tested experimentally. Use of hydrodynamic benefits in forward swimming is not the only means of saving energy. Other energetic benefits might be

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(*i*) less time spent performing escape reactions in large groups, (*ii*) longer foraging time in large groups, (*iii*) greater food capture success, and (*iv*) hydrodynamic benefits in retarding sinking rate.

Results from experiments on gregarious mysids are used here, together with evidence from a range of swarming species, to show that swarming behaviour can have additional benefits to those usually ascribed. Experiments on oxygen uptake by different-sized groups are used to investigate the possible effects of energy saving, while experiments on sinking rate and currents generated by cohesive aggregations are used to identify possible mechanisms by which energy is conserved. If the gregarious habit can be shown to be an important strategy for conserving energy, this would have far-reaching implications for estimating the energetic cost of swimming, feeding, diel vertical migration, and, of course, the total energy budget of the species.

Materials and methods

Oxygen uptake by mysids

The mysid *Paramesopodopsis rufa* forms relatively small aggregations in shallow, nearshore habitats (Ritz 1997). Mature individuals range in size from 9 to 13 mm from the tip of the rostrum to the end of the exopod of the uropod. Collections were made at Taroona Beach (42°56′S, 147°21′E) and Kingston Beach (42°59′S, 147°19′E) (both localities in southeast Tasmania, Australia).

The respirometer was a 24-cm length of perspex tubing (15 cm in diameter), with the ends sealed by means of screw-on caps; total volume of water contained was about 4 L. The experimental section was bounded by two sheets of stainless steel mesh (500 µm), which prevented escape of the mysids. A 3-cm-wide gap at each end of the respirometer between the mesh and the end cap was filled with glass beads 8–12 mm in diameter, which served to straighten flow and reduce turbulence. Also in line was a perspex fitting that snugly housed the oxygen probe (Radiometer E 5046 connected to a Radiometer PHA 934 meter), which was sealed by its O-ring. Calibration of the oxygen probe was checked every day and reset to 100% using air and 0% using water deoxygenated by bubbling nitrogen gas through it. Barometric pressure varied from 751.3 to 772.8 Torr (1 Torr = 133.322 Pa) during the study, and these changes were incorporated into the value for concentration at 100% saturation. Water was circulated through the chamber continuously by means of a peristaltic pump (Eheim type 381, Berlin, Germany), and flow rate was adjusted to 3 $cm \cdot s^{-1}$. Plastic tubing was Tygon (Performance Plastics, Akron, Ohio), which has a low permeability to gases.

The respirometer was run at least once per week without the presence of mysids as a control for background readings of oxygen consumption. The very low readings obtained in these controls could have been due to uptake by bacteria, since the seawater was not sterilised, and (or) to low level consumption by the electrode itself (e.g., see Crisp et al. (1978), who used an identical electrode). The entire respirometer was periodically dismantled and cleaned to remove any possible bacterial buildup.

Mysids were introduced into the chamber through a port in the top fitted with a screw-on cap with an O-ring seal. This port was also used for expelling air bubbles. Prior to each experiment, mysids were allowed to feed for 30 min on powdered fish pellets. The mysids were fed prior to respirometry readings for three main reasons: (*i*) feeding induces tighter aggregation (Ritz 1997), and as I have pointed out previously (Ritz et al. 1997), mysids in the field have lower nearest-neighbour distances than those in laboratory tanks, suggesting better feeding conditions at sea, (*ii*) feeding results in increased oxygen uptake, and I wanted to ensure measurable uptake when using small groups in a large water volume, and (*iii*) these mysids live in shallow (1–6 m) nearshore habitats in which, it seems probable, they are never normally food limited.

After feeding, mysids were gently introduced into the chamber and allowed a further 30 min before oxygen readings commenced. If oxygen readings were erratic in the first hour, thay were ignored and the experiment was allowed to run for a second or sometimes a third hour. Oxygen level in the respirometer never fell to less than 96% saturation during these experiments. Temperature was maintained at 14.4 ± 0.1°C by placing the respirometer in a constant-temperature bath; salinity was 32.9 ± 0.3 psu.

Numbers of mysids used in each test varied from 5 to 100, and the order of group size was selected by reference to a random number table. Five to seven replicates of each group size were conducted. After each experiment, the sex of each mysid was recorded as females carrying embryos, females without embryos, and males, after which the animals were killed rapidly in warm freshwater and dried at 60°C, and their weight was recorded to the nearest 0.1 mg.

Swimming speed

Swimming speed of mysids both in aggregations (100 individuals in tank) and when isolated (10 individuals in tank) was extracted from videofilm. A transparent acetate sheet was taped over the monitor screen and tracks of individuals marked on it. Only those mysids travelling nearly parallel to the screen, as judged by having only one eye in the field of view, were used in this analysis. Average tracking time was 1.5 s (range <1–4 s). Speed was estimated from the number of video frames occupied by the track ($25 \cdot s^{-1}$ for normal playback). Twelve replicates were measured for both isolated and aggregated individuals.

Sinking rate

A mysid was killed by immersion in warm freshwater and released at the top of the water column in the respirometer described above. Rate of sinking was recorded by videofilming, which included a calibrated scale placed inside the tank in the field of view. Groups of either 100, 10, or no mysids were allowed to settle in the tank prior to release of the dead individual, and either no current or one of 3 $cm \cdot s^{-1}$ was circulated through by means of a pump. The passage of the sinking individual did not appear to disturb the swimming mysids, which apparently did not react. Nine replicates were measured for each condition.

Currents produced by swarms

Currents produced by swarms were elucidated by releasing dye streams from a capillary tube positioned just below. A swarm of about 100 mysids fed with powdered fish pellets about 1 h previously to induce tight aggregation (Ritz et al. 1997) was established in a glass tank (40 × 28 × 25 cm) and allowed to settle for 30 min. Temperature was 12.8°C and salinity was 33.9 psu. Red dye (vegetable food dye, 1% solution, Dye manufacturers of Australia, Brisbane) was made up in either distilled water or in the same seawater as in the mysid tank. Dye (0.5 mL) was introduced by hypodermic syringe through plastic capillary tubing with the tip positioned 5 cm above the base of the tank and held in place by a small rock. Mysids did not appear to be affected by this tubing and in every test formed a swarm just above the tip. The plume of dye remained coherent for several minutes after injection, and experiments were recorded on video for later analysis. Water and mysids were replaced after every three injections.

Results and discussion

Oxygen uptake

Individual dry weights ranged from 1.4 to 4.6 mg. Around 50% of the animals used in these experiments were females

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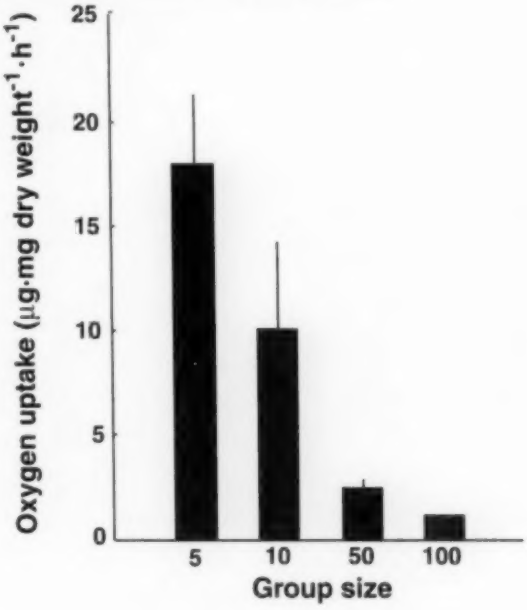
carrying embryos in their brood pouches. Groups of 50 and 100 formed cohesive but unpolarised swarms (nearest-neighbour distances of two to three body lengths, i.e., 20–30 mm) in the respirometer, while groups of 5 and 10 did not aggregate.

A remarkable effect of group size on metabolism was apparent (Fig. 1). Analysis of variance revealed a highly significant effect of group size on oxygen uptake (F = 9.17, df 3,16, $p < 0.001$). Student–Newman–Keuls tests revealed that there was no significant difference between oxygen uptake of nonaggregated groups (5 and 10) and that of aggregated groups (50 and 100) ($p > 0.05$). Aggregations of 50 or 100 mysids, which formed cohesive swarms, consumed 7.2 times less oxygen per milligram weight on average than individuals that did not aggregate. The variance of measurements for the smaller groups was markedly higher than that for the larger groups. Oxygen uptake by swarms (average 1.29 μL O_2·mg dry weight^{-1}) was considerably lower than that reported for a range of mysids at similar temperatures (Smith and Hargreaves 1984), despite the fact that in the present study, mysids were fed just before the experiment, around 50% were females incubating embryos, and *P. rufa* is smaller than all of the species listed by these authors. Oxygen uptake by nonaggregated *P. rufa* (average 9.23 μL O_2·mg dry weight^{-1}) was reasonably close to that of other mysids listed by Smith and Hargreaves (1984), given the factors noted above. When feeding, Antarctic krill consumed oxygen at almost twice the rate of nonfeeding krill (Ikeda 1984). The reason was thought to be a combination of specific dynamic action and the greater activity of feeding animals.

Fish are thought to benefit from vortices shed by neighbours when in polarised school formation (Weihs 1975). If crustaceans gain a hydrodynamic advantage in forward swimming from polarised aggregations, it is possible that when animals form schools as opposed to swarms they might use even less energy. It is perhaps significant that the difference in oxygen uptake between nonswarming and swarming mysids is much greater than that between isolated individual fish and those in schools. Parker (1975) reported that for 14 species, individual fish separated from their school mates consumed oxygen at a rate approximately twice that of members within a school. The differential in oxygen uptake between nonswarming mysids and those in cohesive aggregations was considerably greater. I suggest that the reason for this disparity is that schooling fish almost invariably possess a swim bladder, and retarding sinking rate is energetically inexpensive. The relatively high density of mysids, and most crustaceans (Hargreaves 1981), means that they must work hard to remain in one place in the water column. The fact that aggregated individuals consume much less oxygen per unit weight than nonaggregated individuals suggests that in some way, the swarm or school acts to conserve energy; metabolism of the whole is somehow less than the sum of the parts measured separately. Weihs (1975) suggested that negatively buoyant schooling fish might receive an energy bonus from vortices shed from the tips of pectoral fins of neighbours, which could reduce sinking rate.

Fig. 1. Oxygen uptake by different group sizes of the mysid *P. rufa*. Data are means (±SE) of five replicates.



Swimming speed

One possible short-term mechanism of energy saving in aggregations is slower swimming speed, thereby reducing drag. Results of the swimming speed measurements showed no significant difference when mysids were aggregated or isolated (t test, t = 1.25, df = 22, $p > 0.1$). Average speed was 26 mm·s^{-1}, which agrees closely with speeds of other similar-sized mysids (Hargreaves 1981).

Sinking rate

Sinking rate of a dead mysid (slightly <1 cm·s^{-1}) was not significantly different whether no mysids or an uncohesive group of 10 was present in the water column (t test, t = 0.3, df = 8, p = 0.77) (Fig. 2). This value agrees closely with data for similar-sized krill (Kils 1981). However, when the dead mysid passed through a cohesive swarm of 100 mysids, sinking rate (1.4 cm·s^{-1}) increased significantly (t test, t = 5.38, df = 8, $p < 0.001$). An important result of this experiment is that it reveals that cohesive groups generate a powerful downdraft.

Currents produced by swarms

When dye in freshwater was released into the tank with no mysids present, as expected, the plume rose at a constant rate and spread out at the surface (four replicates). In the presence of a swarm of mysids, the plume remained at the level at which it was released or began to spread sideways, eventually rising around the margin of the swarm (four replicates). This confirms the result obtained in sinking rate experiments that the swarm produces a powerful downdraft that diverts the dye stream and delays its rise to the surface.

In the absence of mysids, dye in seawater settled slowly to the bottom of the tank and remained there (five replicates). In the presence of a swarm of mysids, the plume first travelled upwards (possibly from the force of injection), sank, spread sideways and then spread upwards and sideways again, eventually completing a circle near the margins of the swarm

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Fig. 2. Sinking rate of a freshly dead mysid through different-sized groups of live mysids and in conditions of current (3 cm·s^{-1}) (solid bars) and no current (open bars). Vertical bars represent the SE.

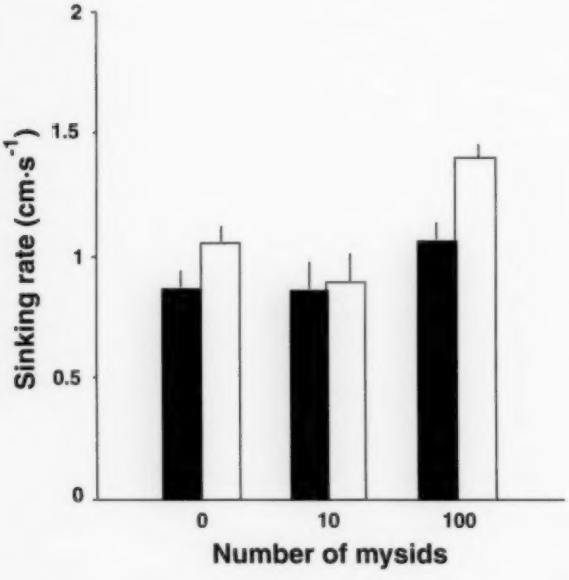
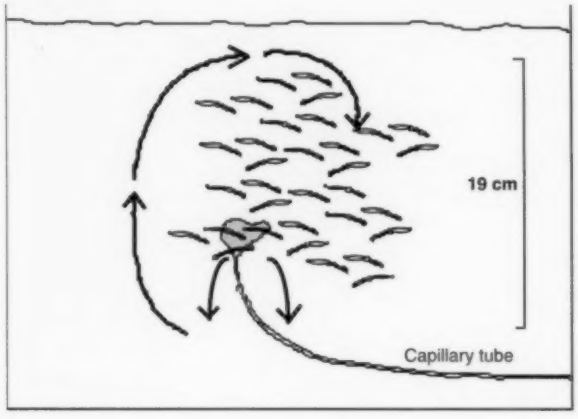


Fig. 3. Currents generated around a mysid swarm. A plume of dye slightly denser than seawater followed the route shown by the arrows. Mysids are not drawn to scale. See the text for additional details.



(approximately 60 cm) in an average of 1.87 min (14 replicates) (Fig. 3). I conclude that combined swimming action generates both a downdraft beneath and an updraft at the margins of the swarm. The latter could be a deflection of the downward current from nearby tank walls or floor, although the aggregation was not less than 50 mm from any solid surface. An alternative explanation is that water is drawn up to replace that driven downwards by the combined swimming actions. These results indicate that a large aggregation is capable of producing very strong currents, even though each of these individuals was only 8–9 mm long.

The implications of these results are wide ranging. If generally applicable to gregarious crustaceans, the oxygen uptake results could invalidate nearly all previous estimates of the metabolic cost of feeding, swimming, and vertical migration of gregarious pelagic invertebrates. Circulation of water around a swarm suggests that individuals could gain height in the water column with very little energy expenditure. However, there is also the problem of simply recirculating the same parcel of water without entraining new water for the purposes of replenishing particulate food and oxygen and dispersing wastes. One way to do this would be for the aggregation to periodically disperse and reform.

Aggregation as an energy conservation strategy

Much has been written about the apparent mismatch between the energy requirements of *E. superba* and energy availability in the water column (Holm-Hansen and Huntley 1984; Quetin et al. 1994). I propose that part of the problem has been a gross overestimate of the energy requirements of krill. This overestimate stems from a history of measurement of rate processes (feeding, oxygen uptake, swimming, etc.) using isolated individuals or small uncohesive groups. I propose that when individuals aggregate into cohesive swarms or schools, the group dynamics produce new emergent properties that cannot be reproduced by scaling up measurements from isolated animals. Use of hydrodynamic conditions within aggregations, e.g., exploitation of vortices shed by neighbours and updrafts produce by combined swimming action, could greatly reduce the energy expenditure.

Swimming

Solitary euphausiids generate a wake that is directed almost vertically downwards (Kils 1981), but those that are swimming with the body held horizontally or that are tethered in this position produce a wake which is directed to the rear and downwards at a shallow angle (e.g., Wiese and Ebina 1995). Note, however, that the direction of the wake can be deflected through about 90° by flexion of the abdomen. The wake is likely to be a source of communication between group members (Wiese and Ebina 1995; Yen and Strickler 1996). Positions directly below a swimming individual are avoided (O'Brien 1989), which is not surprising considering the strong downdraft.

K. Wiese (Zoologisches Institut, University of Hamburg, Hamburg, Germany, personal communication) has shown that the swimming action of tethered *Meganyctiphanes norvegica* produces a propulsion jet directed backwards at a shallow angle. Surrounding this jet are one or two vortex rings within which water particles follow a circular course (Fig. 4). This can perhaps be exploited by individuals to minimise their energy expenditure used to counteract sinking rate. An analogous situation has been observed in lake brine shrimps (B. Hamner, Department of Biology, University of California, Los Angeles, Calif., personal communication). In this case, the shrimps' swimming movements set up directional flow that was deflected vertically by rocks on the bottom producing updrafts. Mysids, many of which are hyperbenthic and have a close association with bottom topography, might also use this technique.

Kils (1981) calculated the energetic cost of swimming in *E. superba* and attributed a high proportion of the total met-

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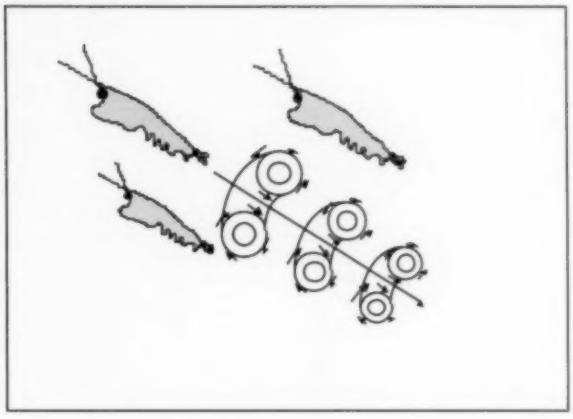
Fig. 4. Vortex rings shed by swimming *M. norvegica*. Data from K. Wiese (Zoologisches Institut, University of Hamburg, Hamburg, Germany, personal communication).

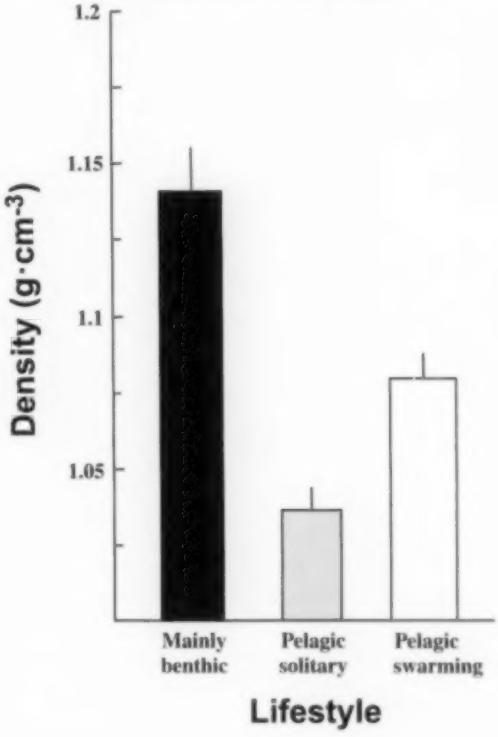


abolic expenditure simply to offsetting the sinking rate (cost of "hovering"). Since it is unrealistic for *E. superba* to cease all visible muscular movement because it would sink quite rapidly to the seabed (Kils 1981), "standard" metabolism is suggested to be equivalent to hovering in one position (Kils 1981; Clarke and Morris 1983; Miller and Hampton 1989). The act of hovering is estimated to require an intake of 0.5% body carbon, which may be as much as one tenth or more of daily energy requirement of 5% carbon (Miller and Hampton 1989). However, this ignores the possible beneficial effects of the presence of other swarm members.

Crustaceans are relatively dense compared with seawater (Hargreaves 1981) and therefore pelagic (including planktonic) species have a buoyancy problem. Most authors have concluded that these crustaceans must work hard to minimise sinking rate. In the case of solitary living and members of gregarious species isolated from their groups, this appears to be the case. Adoption of a steep body angle, up to 55° to the horizontal by *E. superba* (e.g., Kils 1981), *Euphausia pacifica* (Miyashita et al. 1996), and *Thysanoessa raschii* (Price 1989), is probably an expression of the need to increase lift generation. Miyashita et al. (1996) found an inverse relationship between body angle and speed in *E. pacifica*, which accords with observations by other authors. For example, when schooling, which usually coincides with faster swimming or facing into moderate currents, euphausiids and mysids adopt a more horizontal attitude in the water (Strand and Hamner 1990; D.A. Ritz, personal observation). This suggests that the school itself is a source of updraft by which members can minimise the effort needed to retard sinking. Presumably, individuals could only exploit shed vortex rings when in parallel orientation, i.e., schooling as opposed to swarming, and this could be why animals in schools adopt a horizontal body attitude, while swarming individuals must adopt a positive angle of attack.

Hargreaves (1981) estimated the cost of lift production in mysids to be 2.2 times the minimum cost of transport, although any energy bonus from group dynamics was neglected. Clearly, pelagic species need to reduce their underwater weight by some means, e.g., decreasing calcium in the

Fig. 5. Density of crustaceans in relation to lifestyle: benthic (solid bars), solitary pelagic (hatched bars), and gregarious pelagic (open bars) forms. Vertical bars represent the SE. Examples have similar-shaped body forms (mainly mysids, euphausiids, and decapods) and are taken from Lowndes (1942) (*Hemimysis lamornae*), Morris (1972) (*Heterocarpus grimaldii, Acanthephyra pelagia, A. purpurea, Eucopia sculpticauda*), Childress and Nygard (1974) (*Sergestes phorcus, S. similis, E. pacifica, Gnathophausia ingens, G. gigas, G. gracilis*), Greenlaw (1977) (*E. pacifica*), Spaargaren (1979) (*Praunus flexuosus, Palaemon serratus, P. squilla, Pontophilus spinosus*), Williams (1980) (*Munida gregaria*), Kils (1981) (*E. superba, M. norvegica, Crangon crangon*), and Davenport (1994) (*Phronima sedentaria*).



cuticle (Kils 1981). This has led to a large and significant difference in density between benthic and pelagic species (Fig. 5). However, such strategies require a reallocation of energy away from other processes such as growth and reproduction. If schooling behaviour is a strategy to offset sinking and conserve energy, then it can be hypothesised that gregarious pelagic species can afford to be denser than their solitary pelagic counterparts. This does indeed seem to be the case (Fig. 5). Examples in this figure are restricted to elongated shrimp-shaped species (mysids, euphausiids, and decapods) larger than about 10 mm. Animals smaller than this are subject to rather different hydrodynamic environments, e.g., at Reynolds numbers of less than 40, swimming zooplankters do not generate vortices (Vogel 1981).

Hamner et al. (1989) described the ontogeny of *E. superba* in relation to sea ice. Prior to the furcilia IV stage, krill larvae live a solitary life. Aggregation is apparently cued by

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Fig. 6. Relationship between food capture success of the gregarious mysids *P. rufa* expressed as mean (±SE) dry weight of food per 10 stomachs and swarm size at two feeding regimes: (A) 5% biomass (open bars) and (B) 25% biomass (hatched bars). Reprinted from Ritz (1997) with the permission of Cambridge University Press, Cambridge, U.K.

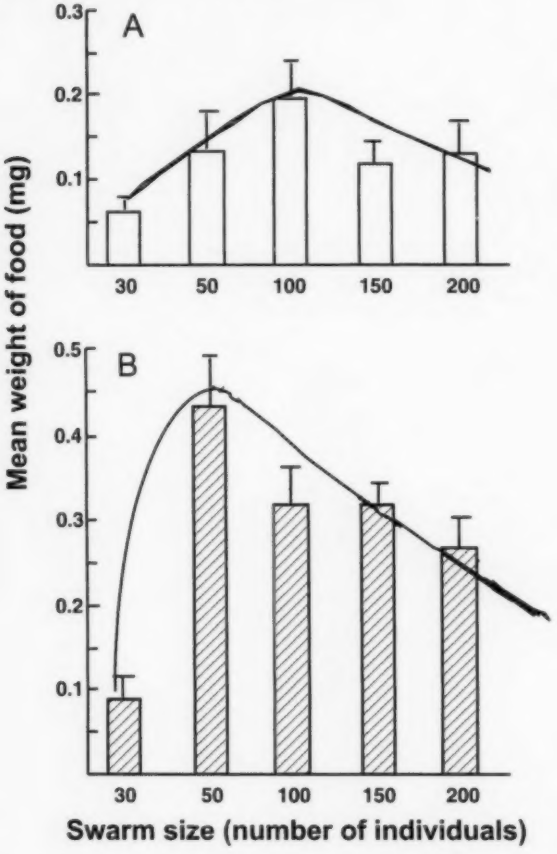
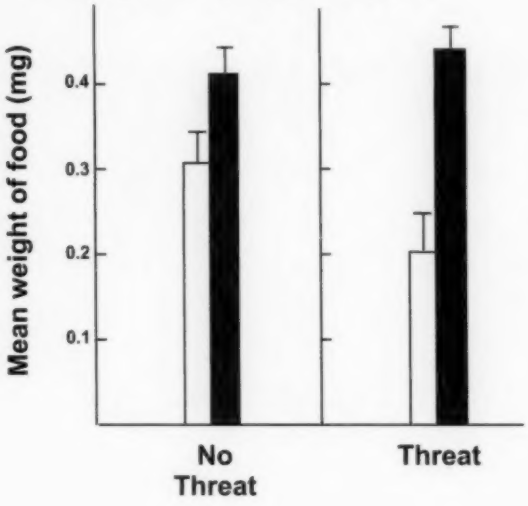


Fig. 7. Relationship between food capture success (dry weight per 10 stomachs) and swarm size in conditions of threat, i.e., presence of fish and no threat. Large swarm (solid bars), 500 mysids; small swarm (open bars), 100 mysids. Vertical bars represent the SE. Reprinted from Ritz (1997) with the permission of Cambridge University Press, Cambridge, U.K.



floating sea ice when larvae reach a size of around 10 mm. I hypothesise that this is the size beyond which the cost of resisting sinking becomes too great to remain solitary. If this theory is correct, a corollary is that there is an imperative for warmwater species to aggregate at much smaller sizes because of the effect of temperature on water viscosity. A rise in temperature from 0 to 30°C decreases viscosity by more than 50%.

It is tempting to suggest that the only possible strategy for a fundamentally demersal fish with no swim bladder (Antarctic silverfish, *Pleurogramma antarcticum*) to adopt pelagic life is to live in schools. Obligate schooling is otherwise rare among fish in the Southern Ocean (Knox 1994). A comparison of oxygen uptake between isolated and schooling *P. antarcticum* would be very interesting and is predicted to mirror that shown for mysids rather than that shown for fish with swim bladders (e.g., Parker 1975).

Feeding

Many authors have estimated in situ feeding rates of Antarctic krill by measuring gut fluorescence of freshly caught animals (Pakhomov et al. 1997), by means of laboratory experiments using average ambient levels of chlorophyll *a* as food in tanks of various sizes (e.g., Antezana et al. 1982; Price et al. 1988), and by faecal egestion experiments on freshly caught animals (Pakhomov et al. 1997). In general, estimated field ingestion rates are much higher than those measured in laboratory tanks (Quetin et al. 1994). This has been attributed largely to an effect of confinement and tank size. However, the possibility that these higher values arise because krill in the field are feeding in aggregations seems not to have been considered. Where two methods (uptake in tanks versus faecal egestion) have been directly compared (e.g., Pakhomov et al. 1997), the faecal egestion technique yielded a threefold higher daily ration. The authors ascribed this to predation on micro- and meso-zooplankton in addition to phytoplankton. Alternatively, this difference could be accounted for by the much higher feeding efficiency within aggregations compared with that by isolated krill or uncohesive small groups which are usually employed in laboratory feeding experiments. Antezana et al. (1982) used high numbers and high densities in their feeding experiments, but it is not clear whether the krill formed cohesive aggregations. Previous work on gregarious mysids demonstrated that small groups captured food nearly 5 times less successfully than larger groups (Ritz 1997) (Fig. 6). In this case, per capita food availability was equal for all swarms, but the differential between small and large groups was preserved when much higher concentrations of food were supplied. Moreover, the differential capture success was magnified when mysid swarms were exposed to a predatory threat (Fig. 7). Reasons for the improved capture success by larger groups were speculated to be (*i*) greater time available for feeding and (*ii*) that individuals in small groups are more "nervous" and swim faster along straighter paths (D.A. Ritz, personal ob-

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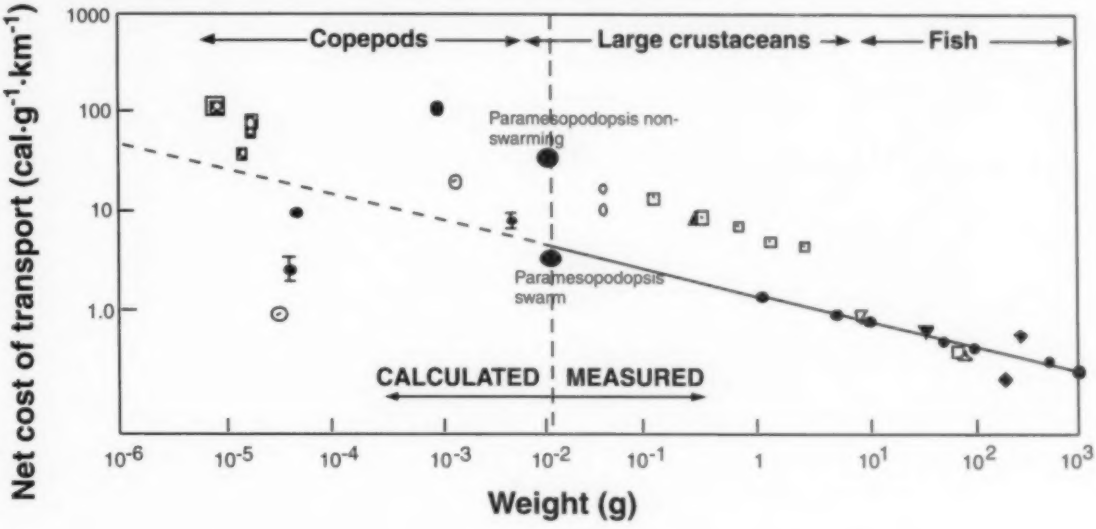
Fig. 8. Net cost of transport as a function of body weight for swimming fish and crustaceans. Modified from Morris et al. (1990) with the permission of NRC Research Press, National Research Council of Canada, Ottawa, Ont.



servation), presumably because more time is allocated to alertness to predator approach and less to foraging.

Greater capture success by individuals in aggregations than by isolated individuals might also be a result of hydrodynamics within aggregations. Vortices shed by many grouped animals, each of which has five pairs of reciprocating swimming appendages, create a highly complex environment within a swarm or school. Characteristic nearest-neighbour distances of 0.5–0.6 body length in *E. superba* (O'Brien 1989) have not arisen by chance. These spacings may optimise communication between individuals, maximise beneficial use of shed vortices in retarding sinking rate and perhaps in forward swimming, and also facilitate optimal capture of suspended particles. Vortices generated by swimming animals may persist for several seconds and hence could impart useful information to animals encountering them (e.g., Yen and Strickler 1996). Such information could include identity of the creator of the vortex trail, time since it passed, speed, and direction. Ritz and Metillo (1998) tested the hypothesis that the swarming configuration of mysids (individuals cohesive but not polarised) was beneficial for detaining particles longer and therefore maximising the possibility of capture than when individuals adopted a school (polarised) configuration. They did not prove their hypothesis, but the group size was small (13 individuals) and food concentration was high in their experiment. They speculated that if food concentration had been both patchy and low, there might have been advantages in adopting a swarm configuration. It can be envisaged that any food-sized particle within a dense swarm of krill would have very little chance of avoiding ingestion, which is probably why large plankton net catches of krill are nearly monospecific.

Vertical migration

Many authors have calculated the costs of vertical migration by plankton and micronekton (e.g., Vlymen 1970; Torres and Childress 1983). These have mostly been estimated theoretically from energy expenditure required to overcome drag or empirically from measurement of oxygen uptake by usually solitary, swimming individuals. Early calculations (e.g., Vlymen 1970) suggested that diel vertical migration was not costly energetically. Torres and Childress (1983) concluded from work on the gregarious euphausiid *E. pacifica* that diel vertical migration was a very costly process. However, if *E. pacifica* migrates in cohesive swarms or schools, this could considerably reduce the expenditure.

To illustrate the possible consequences of ignoring the effect of swarming, I present a figure modified from Morris et al. (1990) showing net cost of transport for a range of crustaceans and fish. They concluded that the cost of transport for crustaceans in relation to body mass falls on a line with a slope similar to that for fish but with a higher intercept (Fig. 8). However, I have added data for the mysid *P. rufa* when swarming and when not swarming. When not in aggregations, *P. rufa* data conform quite closely to data for other similar-sized crustaceans. In contrast, when in an aggregation, the cost of transport falls close to the trend line for fish. This suggests that swarming crustaceans, like schooling fish, are not working hard to resist sinking and, in fact, gain an energy bonus from group dynamics. If gregarious animals migrate as cohesive groups, as acoustic evidence suggests, then the cost of transport could be much less than has been claimed. Torres and Childress (1983), for example, measured oxygen uptake by solitary *E. pacifica*, a swarming euphausiid, and estimated that an individual of 6.9 mg dry weight would expend about 0.41 cal (1 cal = 4.1868 J) (9.24 μL of oxygen) making the return trip from daytime depth to the surface and back, a total distance of around 600 m. This is approximately 23.8 $cal \cdot g^{-1} \cdot km^{-1}$ or 6 times more than would be the case for *P. rufa* if it made the same migration as a cohesive aggregation. Of course, *P. rufa* does not migrate vertically over such distances (Fenton 1992), but the point at issue is, by aggregating into swarms or schools, great energy savings are possible.

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Energy budget of *E. superba*

Clarke and Morris (1983) presented a preliminary energy budget for *E. superba*. This was subsequently updated by Quetin et al. (1994). In most cases, these budgets use feeding and (or) respiration data obtained using individuals isolated from conspecifics. There is a considerable discrepancy between calculated energy requirement and energy available in the water column. One of the major conclusions was that *E. superba* required a daily ration of around 5% carbon. This translates into a daily food intake of 144 µg of chlorophyll *a* or, at characteristic ambient phytoplankton concentrations, a necessity to filter 144 L (6 $L \cdot h^{-1}$ continuously) for an animal of 245 mg dry weight (Clarke and Morris 1983). Holm-Hansen and Huntley (1984) concluded from their study that at typical krill densities, *E. superba* could obtain sufficient energy from food to satisfy its metabolic requirements and to grow and reproduce. Subsequent studies suggested that higher feeding rates than reported earlier were possible (e.g., Price et al. 1988), but even so, in dense swarms, the available food would be barely enough for maintenance and would not permit growth or reproduction. But these estimates of daily energy requirements are based on oxygen uptake and ingestion rates of isolated individuals or small uncohesive groups. As argued earlier, these ignore any possible energy subsidy provided by group dynamics. As demonstrated for gregarious mysids, this can be considerable.

In conclusion, extrapolating metabolic costs of such processes as feeding, swimming, and vertical migration from measurements made on isolated individuals of species that are normally gregarious will only produce artifacts. I propose that the process of swarming and schooling of individuals into ordered ranks results in emergent properties that cannot be reproduced by simply scaling up measurements made on individuals separated from the group. This would not be a surprising claim if it were made for schooling fish. Claims of hydrodynamic advantages of schooling in fish date back at least 40 years, although experimental proof is elusive. However, it has been demonstrated many times that oxygen uptake by individual fish separated from their school increases around twofold (e.g., Parker 1975). This has been attributed both to nervous, jerky swimming in isolates and to hydrodynamic benefit when in formation. Differences in oxygen uptake by aggregated and nonaggregated mysids, however, are far greater. My suggestion for explaining this is that crustaceans benefit hydrodynamically from forces that serve to reduce their sinking rate when in swarms and perhaps also from forces assisting forward swimming when they are schooling. Crustaceans are particularly dense relative to seawater. That they need to work hard to maintain position when swimming slowly is, I believe, clearly illustrated by their adoption of a steep body angle to the horizontal, a position that maximises generation of lift. In schools, when individuals are usually swimming faster, the body is held horizontally, suggesting that lift generation is much less important. Lift generation by altering body angle is, of course, unimportant in fish with swim bladders, which might explain the smaller differences in oxygen uptake between schoolers and isolates. Weihs (1975) suggested that negatively buoyant fish might gain uplift from vortices shed by the pectoral fins of neighbours, although this apparently has never been tested experimentally. Ritz et al. (1997) noted that in laboratory tanks, mysid swarm volumes contracted rapidly after feeding. They attributed this to the safety imperative once hunger demands had been met. However, it may be that a trade-off between the need to capture food and the need to resist sinking demands a return to close packing as quickly as possible. Modelling the hydrodynamics of five pairs of metachronally reciprocating pairs of pleopods and the interaction with neighbouring animals is a daunting task but one that could be extremely rewarding.

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Demography and life cycle of Antarctic krill, *Euphausia superba*, in the Indian sector of the Southern Ocean: long-term comparison between coastal and open-ocean regions

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Abstract: Size/age composition and reproductive status of Antarctic krill, *Euphausia superba*, in the central part of the Indian sector of the Southern Ocean, e.g., the Cooperation Sea (Prydz Bay region) and the Cosmonaut Sea, during austral summers 1977–1990 were summarized to estimate growth rates, longevity, reproduction, recruitment, life span, and mortality rates. The life span of Antarctic krill exceeds 5 years in both the Cosmonaut and Cooperation seas. The age composition of the southern and northern groupings differs markedly, with substantial reduction in numbers of early age groups in the northern grouping. Long-term observations of spawning success, recruitment, and age composition suggest that a self-sustained grouping of krill persists in the Cooperation Sea south of the Antarctic Divergence. However, periodic gene flow via recruits from surrounding regions most probably accounts for the lack of spatial genetic differences between the Cooperation Sea and adjacent areas, thus preventing the establishment of an isolated subpopulation in the region investigated. The major factor responsible for the substantial interannual variability in krill dynamics appears to be macroscale oceanographic and atmospheric circulations, which determine a level of environmental isolation of the Cooperation Sea from adjacent waters.

Résumé : Nous avons synthétisé des données sur la composition par taille/âge et l'état reproductif du krill antarctique, *Euphausia superba*, dans le centre du secteur indien de l'océan Austral, notamment la mer de la Coopération (région de la baie de Prydz) et la mer des Cosmonautes, pendant les étés australs de 1977 à 1990, afin d'estimer le taux de croissance, la longévité, la reproduction, le recrutement, la durée de vie et le taux de mortalité de ce crustacé. La durée de vie du krill antarctique dépasse 5 ans dans la mer de la Coopération et la mer des Cosmonautes. La composition par âge des regroupements du nord et du sud diffère de façon marquée, le regroupement du nord présentant une réduction importante de l'effectif des groupes des premiers stades. Des observations de longue durée sur le succès de reproduction, le recrutement et la composition par âge signalent qu'un regroupement stable de krill persiste dans la mer de la Coopération au sud de la divergence antarctique. Toutefois, des flux géniques périodiques, via des recrues provenant des régions avoisinantes, expliquent probablement l'absence de différences génétiques spatiales entre la mer de la Coopération et les régions adjacentes, ce qui empêche l'établissement d'une sous-population isolée dans la région à l'étude. Le principal facteur responsable de l'importante variabilité interannuelle dans la dynamique du krill semble être une circulation océanique et atmosphérique sur une macro-échelle, qui crée un certain isolement environnemental de la mer de la Coopération par rapport aux eaux adjacentes.

[Traduit par la Rédaction]

Introduction

It is now recognized that Antarctic krill, *Euphausia superba*, is an opportunistic species able to adapt its life cycle to changing environmental conditions, which vary spatially in the different regions around the Antarctic continent (Makarov and Spiridonov 1993; Knox 1994). As a consequence, the most fruitful approach to studying the life cycle of krill has been suggested to be that which takes into account the specific background environmental conditions in the area under investigation (Makarov and Spiridonov 1993). Traditionally, studies on Antarctic krill were concentrated in the South Atlantic, particularly in the Scotia Sea, around the Antarctic Peninsula and South Georgia. This was a reflection of the persistence of large stocks of this species in these areas (Knox 1994). At present, as a result of the multicountry effort, the most comprehensive data sets concerning different aspects of Antarctic krill biology are only available for some areas off the Antarctic Peninsula (Knox 1994; Loeb et al. 1997; Siegel et al. 1997).

In contrast with the South Atlantic, krill distribution has been poorly, or only occasionally, studied in other regions of the Southern Ocean (Miller and Hampton 1989; Makarov and Spiridonov 1993). Although this is particularly the case in eastern Antarctica, there are some regions apart from the South Atlantic sector where krill dynamics have been studied regularly and over a long period of time. One such area

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is the central part of the Indian sector of the Southern Ocean, namely the Cooperation Sea (Prydz Bay region) and the Cosmonaut Sea (e.g., Hosie et al. 1988; Pakhomov 1995). To my knowledge, during the past two and a half decades, substantial scientific efforts of at least five countries (Japan, France, South Africa, Australia, and the former U.S.S.R.) were concentrated in these regions with regard to krill research. However, although the major research findings of the first four nations are relatively well documented (e.g., Miller 1986; Shirakihara et al. 1986; Hosie 1994), the substantial data sets collected during the former U.S.S.R. expeditions are either not published at all or published in Russian journals and books, which are largely unaccessible to world krill scientists. For example, for 15 years (1974 and 1977–1990), the Southern Scientific Research Institute of Marine Fisheries and Oceanography (YugNIRO, Kerch, Ukraine (former U.S.S.R.)) carried out annual multidisciplinary research on the pelagic ecosystem functioning, with a particular emphasis on Antarctic krill, in the Cooperation and Cosmonaut seas covering the area between 30 and 90°E and south of 60°S (Pakhomov 1995). Since 1981, this research has been complemented by efforts from other countries in the Prydz Bay region, particularly within the framework of the international BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks) programme (e.g., Williams et al. 1983; Miller 1986; Miquel 1991). After 1990, the only country that has persisted with research in this area is Australia (Australian Antarctic Division, Hobart).

One of the most common features of the macroscale distribution of Antarctic krill is the increase in density in two different zones of the Southern Ocean (Makarov and Spiridonov 1993). The southern circumpolar belt of high krill density is restricted to the Antarctic Coastal Current (East Wind Drift), north of the shelf edge and above the upper part of the continental slope. The northern belt of high krill density is associated with the frontal zones (Maslennikov 1980, 1995), where waters of high latitudes are mixed with waters of the Antarctic Circumpolar Current. Apart from the Weddell Sea where the northern belt is strongest, it is not as continuous as the southern one but can be distinctly identified around the Antarctic Continent in the Bellingshausen, Lazarev, Riiser-Larsen, Cosmonaut, Cooperation, and Dumont D'Urvile seas (e.g., Makarov and Sysoeva 1983; Iganake et al. 1984; Miller 1986).

Unlike the southern belt of high krill densities, a classic asymmetrical pattern in the distribution of the northern belt of high krill densities is well documented (Marr 1962; Mackintosh 1973). In the Atlantic sector, waters with high krill biomass are associated with the northern branch of the Weddell Gyre, which deflects southward east of Bouvet Island (Marr 1962; Maslennikov 1980). Accordingly, krill, which is found in the Atlantic sector as far north as 51°S, is not generally recorded north of 59–60°S in eastern Antarctica (Miller and Hampton 1989). However, krill that belong to the northern branch of the Weddell Gyre (a phenomenon called the Weddell Drift) may be traced in the Indian sector of the Southern Ocean as far east as the Cosmonaut Sea, which lies to the west of the Cooperation Sea (Bibik et al. 1988; Pakhomov 1995).

This paper has two main purposes: firstly, to provide a comprehensive synthesis of Antarctic krill demography and long-term variability in some demographic parameters in the central part of the Indian sector of the Southern Ocean with a particular effort to incorporate the Russian and Ukrainian work on krill, and secondly, to study relationships of the krill stock in the Prydz Bay region with similar stocks in adjacent (west, east, and north) regions.

Environment

Macroscale biotopes: water and frontal structure

Multidisciplinary, long-term observations of the environmental parameters of the central part of the Indian sector of the Southern Ocean have identified differences between the Cooperation Sea and the regions adjacent to it. Based on the results of statistical volumetric temperature/salinity analyses within the top 2000 m, three macroscale biotopes south of 54°S between 20 and 120°E have been identified (Lanin 1993). The Cooperation Sea (between 50 and 85°E) has been characterized by the highest heat content of the water masses (27.1×10^{17} kcal) compared with the Riiser-Larsen and Cosmonaut seas (16.3×10^{17} kcal) and Davis and Mawson (15.1×10^{17} kcal) seas (Lanin 1993). This appears to be the result of advection of warm deep waters into the Cooperation Sea within a branch of the Antarctic Circumpolar Current, which is deflected south by the Kerguelen Ridge (Lutjeharms 1982; Saruchanyan and Smirnov 1986; Lanin et al. 1987). Lanin (1993) showed that the Cooperation Sea is the only region between 20 and 120°E where the 2°C isotherm crosses 60°S and the 1.5°C isotherm is recorded in its southernmost position (Fig. 1). The Cooperation Sea reflected this advection with temperatures of 1.4–2.2°C and salinities of 34.4–34.8‰, the lowest volume of the cold winter layer, and the thinnest layer of the Antarctic surface water when compared with the west and east regions (Fig. 2). It has been suggested that the Cooperation Sea is well isolated from the deep waters of the Davis and Mawson seas, while the deep waters from the Cooperation Sea may, during some years, be advected into the Cosmonaut Sea via the Antarctic Coastal Current (Lanin 1993). Satellite tracking of icebergs also confirmed the spatial separation between the Cooperation and Davis and Mawson seas (Tchernia and Jeannin 1984). Besides the advection of deep waters into the Cosmonaut Sea, two major regions of their transformation in the Cooperation Sea were identified. The first region was associated with the Antarctic Divergence (AD) region (63–66°S), where warm deep waters break through the cold winter layer and reach the surface (Fig. 3). The second region coincides with the southern part of the Cooperation Sea, where deep waters mixed with the cold shelf waters (Fig. 3) (Pakhomov and Karpenko 1992; Lanin 1993). As a consequence, in both areas, subsurface frontal zones are found (Klyausov and Lanin 1987, 1988). It is suggested that these two energetically active regions may be responsible for the formation of coastal and open-ocean polynyas in the Cooperation Sea during the austral winter and spring similar to the Weddell polynya (Buinitski 1973; Dmitrash 1975; Martinson et al. 1981). Furthermore, in the region of the AD, the upwelled transformed deep waters create north to south movement of surface waters (Fig. 3). These transformed Antarctic surface waters converge with surface shelf waters south of the AD and with nontransformed Antarctic surface water north of

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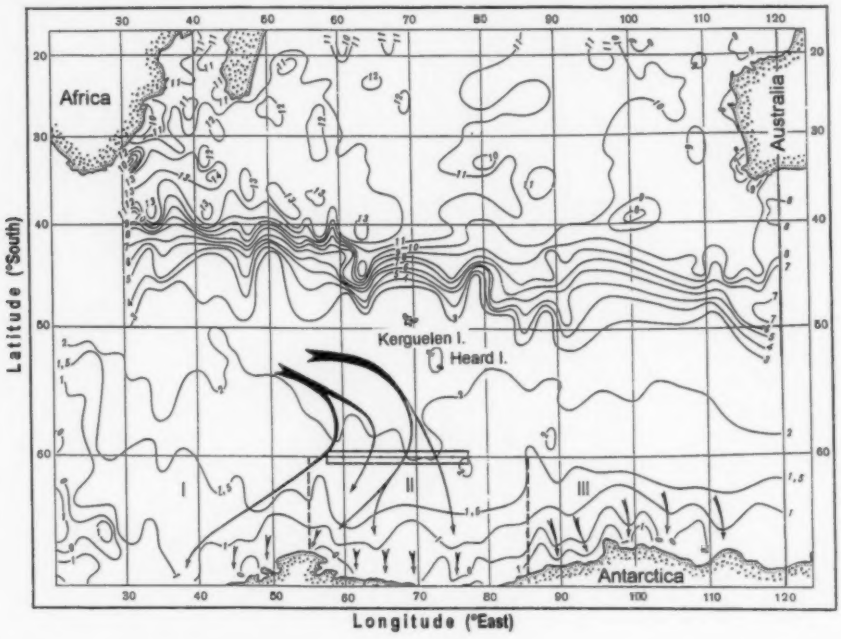
Fig. 1. Temperature distribution at 500 m depth during the summer season (December–March) in the Indian sector of the Southern Ocean (modified from Lanin 1993). Broken lines separate the western (I, Riiser-Larsen and Cosmonaut seas), central (II, Cooperation Sea), and eastern (III, Davis and Mawson seas) regions. Arrows indicate advection of the warm intermediate waters. The rectangle shows the area that was used to calculate an advection of deep waters into the Cooperation Sea.



the AD at approximately 67 and 62°S, respectively (Fig. 3) (Pakhomov and Karpenko 1992). Therefore, four surface macroscale biotopes persist in the region of the Cooperation Sea. This has subsequently been confirmed by zooplankton community structure studies (e.g., Pakhomov 1993; Hosie 1994).

Currents and circulation patterns

Major elements of the geostrophic circulation in the Cooperation Sea, observed over the period from 1977 to 1990, have appeared to be a stationary cyclonic circulation centered at approximately 66°S and 70°E, e.g., north of the Prydz Bay, and anticyclonic menders north of the AD (Fig. 4) (Smith et al. 1984; Lanin et al. 1987; Bibik et al. 1988). Although charts of the geostrophic circulation showed clear southward movement of water in the eastern part of the Cooperation Sea, iceberg and sea ice buoy trajectories have confirmed the northeast movement of water, which reaches 61°S before turning eastward (e.g., Kumagori and Yanagawa 1958). In the coastal region, the westward transport of water along the shelf/upper slope is clearly evident. This movement has subsequently been confirmed by satellite tracking of icebergs, sea ice buoys, and current meter moorings (Tchernia and Jeannin 1984; Hodgkinson et al. 1988; Danilov and Guretsky 1993). In the Cosmonaut Sea region, waters moving eastward north of 64°S turn southward at approximately 50°E, where they join the Antarctic Coastal Current, which moves westward from the Cooperation Sea. Water masses moving along the coast of the Cosmonaut Sea partially cross the Gunnerus Ridge and are partially deflected northward at approximately 30°E (Treshnikov 1964; Maslennikov et al. 1986; Bibik et al. 1988). Iceberg and sea ice buoy trajectories are in very good agreement with the above circulation pattern (Fig. 4) (e.g., Tchernia and Jeannin 1983).

The above brief synthesis of the water structure and general circulation patterns in the central part of the Indian sector of the Southern Ocean thus suggests some prerequisites for the macroscale semi-isolation between the Cosmonaut, Cooperation, and Davis seas (Lanin 1993).

Krill dynamics

Distribution, abundance, and biomass

Macroscale spatial distribution of Antarctic krill in the Cooperation Sea over the period 1977–1990 and in the Cosmonaut Sea between 1987 and 1989 has been characterized by a high degree of similarity between years. This is probably a reflection of the stationary environmental conditions in the regions investigated (Pakhomov 1991; Samyshev 1991). Although krill have been found throughout the entire region south of 59°S, the highest biomass levels have always been associated with the frontal zone between the shelf waters and transformed Antarctic surface waters along the shelf break/upper continental slope (Figs. 5 and 6) (Miller 1986; Hosie et al. 1988; Pakhomov 1991). Mesoscale distribution patterns during different years generally reflect the mesoscale variability in circulation patterns and as a consequence will not be discussed here.

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Fig. 2. Block diagram of waters with different temperature and salinity characteristics in the western (I), central (II), and eastern (III) regions in the Indian sector of the Southern Ocean (modified from Lanin 1993). 1, summer Antarctic surface water; 2, winter Antarctic surface water; 3, warmest intermediate waters; 4, deep intermediate water; 5, boundary between the Antarctic surface water and deep intermediate water; 6, Antarctic bottom water.

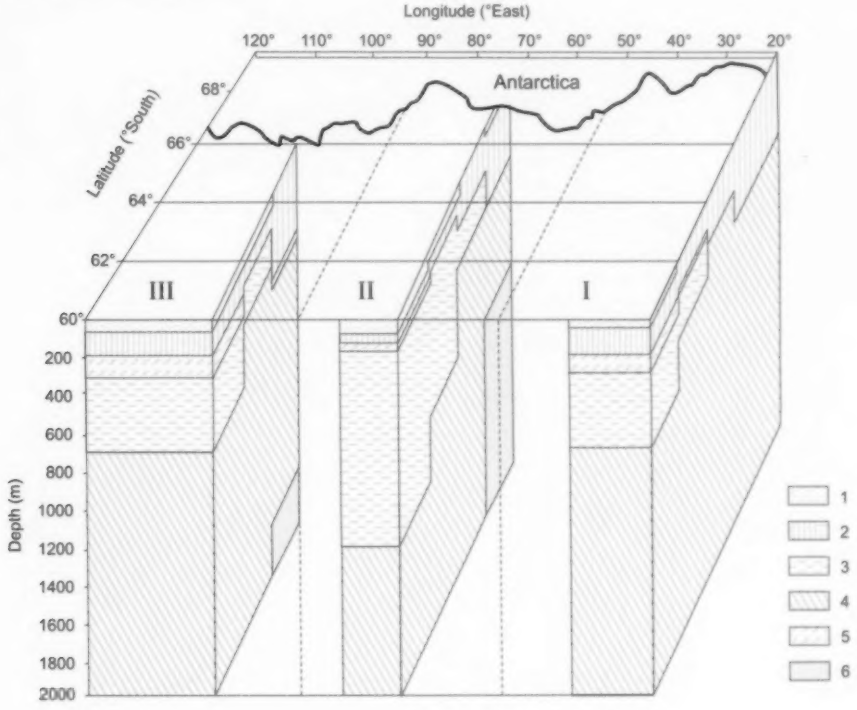

Fig. 3. Diagram of water movements and water modifications in the Cooperation Sea (modified from Pakhomov and Karpenko 1992). SW, shelf waters; TSW, transformed shelf waters; SAW, surface Antarctic water; TSAW, transformed surface Antarctic water; SCZ, southern convergence zone; NCZ, northern convergence zone.

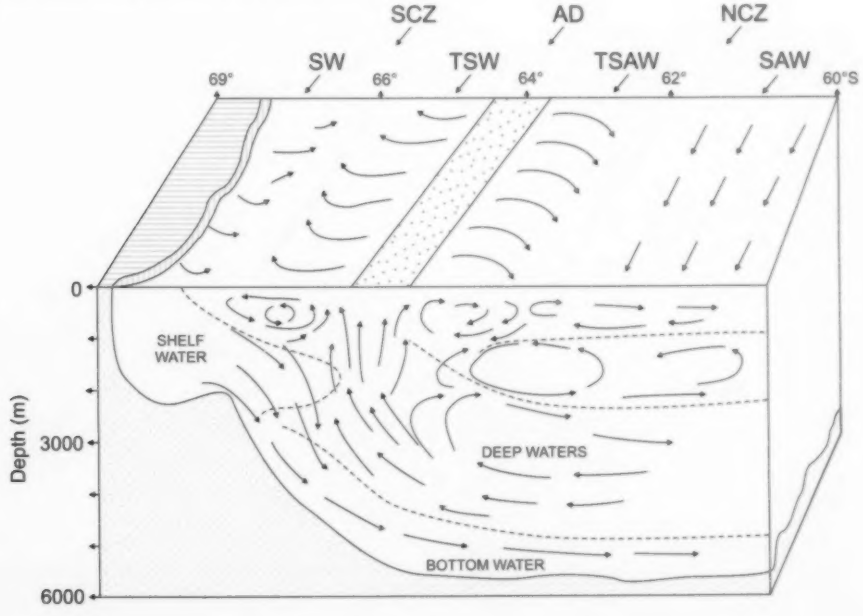

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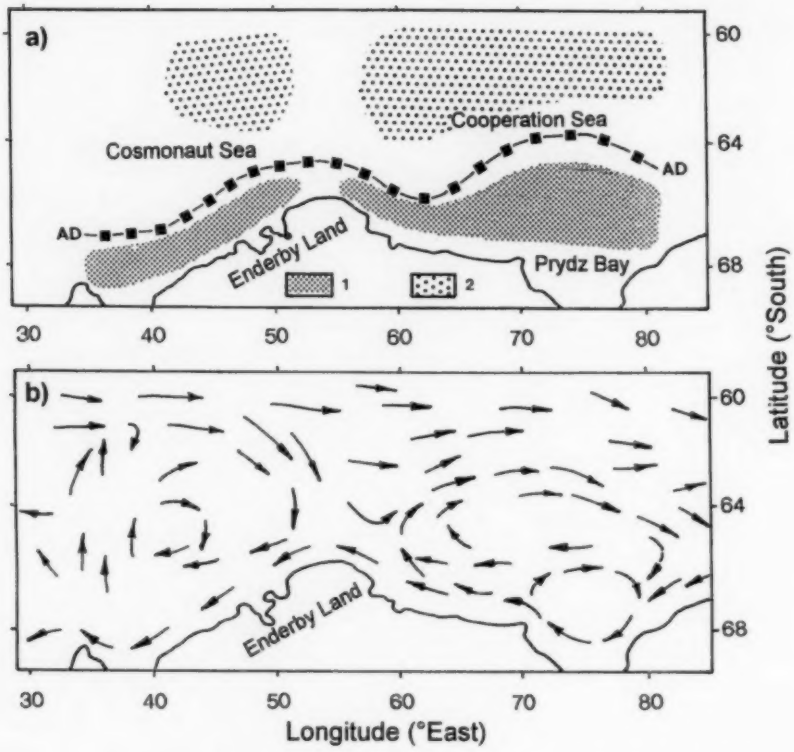
Fig. 4. (*a*) Position of the sampling areas and (*b*) the generalized surface circulation in the central part of the Indian sector of the Southern Ocean (modified from Treshnikov 1964; Bibik et al. 1988; Danilov and Guretsky 1993). 1, southern sampling area; 2, northern sampling area.



In addition to the southern belt of high krill density, enhanced krill biomass levels have also been observed periodically north of the AD between 59 and 63°S, in the eastern part of the Cosmonaut Sea, and in the western and eastern parts of the Cooperation Sea. These regions roughly coincide with the northern surface convergence region (Miller 1986; Miquel 1991; Pakhomov 1993). Data obtained from net sampling indicate that this belt is not as consistent as the southern belt, although it has clearly been identified during periods when substantial sampling effort was undertaken in this area and has also regularly been observed during continuous acoustic studies (e.g., Shirakihara et al. 1986; Higginbottom et al. 1988; Bibik and Yakovlev 1991). Although krill densities in the northern belt are generally lower than krill densities found south of the AD, during years when substantial sampling effort was undertaken, densities between the two regions were similar (Bibik et al. 1988; Pakhomov 1993).

Table 1 presents average Antarctic krill densities during selected surveys estimated from pelagic net trawl catches. In the Cooperation Sea during the austral summer, average krill abundance and biomass ranged from 3.3 to 346 individuals·1000 m^{-3} and from 2.03 to 170.18 g wet weight·1000 m^{-3}, respectively, in the top 200-m layer. These estimates agree with those obtained elsewhere in the Southern Ocean (Hosie et al. 1988; Miller and Hampton 1989). In the Cosmonaut Sea, lower krill densities and biomass ranging from 16.4 to 122.3 individuals·1000 m^{-3} and from 4.81 to 39.26 g wet weight·1000 m^{-3}, respectively, have been identified in the top 200-m layer (Table 1).

Comprehensive acoustically estimated values for average biomass and total stock in the Cooperation Sea are available for the period 1977–1993 (Table 2). The most complete data set is available for the southern part of the region. Here, total stock estimates ranged from 1.15×10^6 t in January–February 1993 to 25×10^6 t in February–March 1977 and biomass densities from 7.7 to 187.7 $g \cdot m^{-2}$ (Table 2; Fig. 7). Average total stock and biomass density over the 17-year period were 5.12×10^6 t and 50.73 $g \cdot m^{-2}$, respectively. In the oceanic region adjacent to the Cooperation Sea, total stock estimates ranged from 2.44×10^6 t in December 1983 to 75×10^6 t in February–March 1977 and biomass densities from 10.5 to 100.8 $g \cdot m^{-2}$ (Table 2; Fig. 7). Average total stock and average biomass density over the 8-year period were 25.28×10^6 t and 35.6 $g \cdot m^{-2}$, respectively. It is notable that although the average total stock was different for the regions south and north of the AD, the average biomass in the two regions was of the same order of magnitude.

The above long-term acoustic survey data indicate that the total krill stocks were generally higher during the 1977–1978 period of observations. Thereafter, krill stocks remained relatively constant, with small increases during summer seasons of 1983–1984 and 1990 (Fig. 7). A similar pattern was also observed for the average biomass densities,

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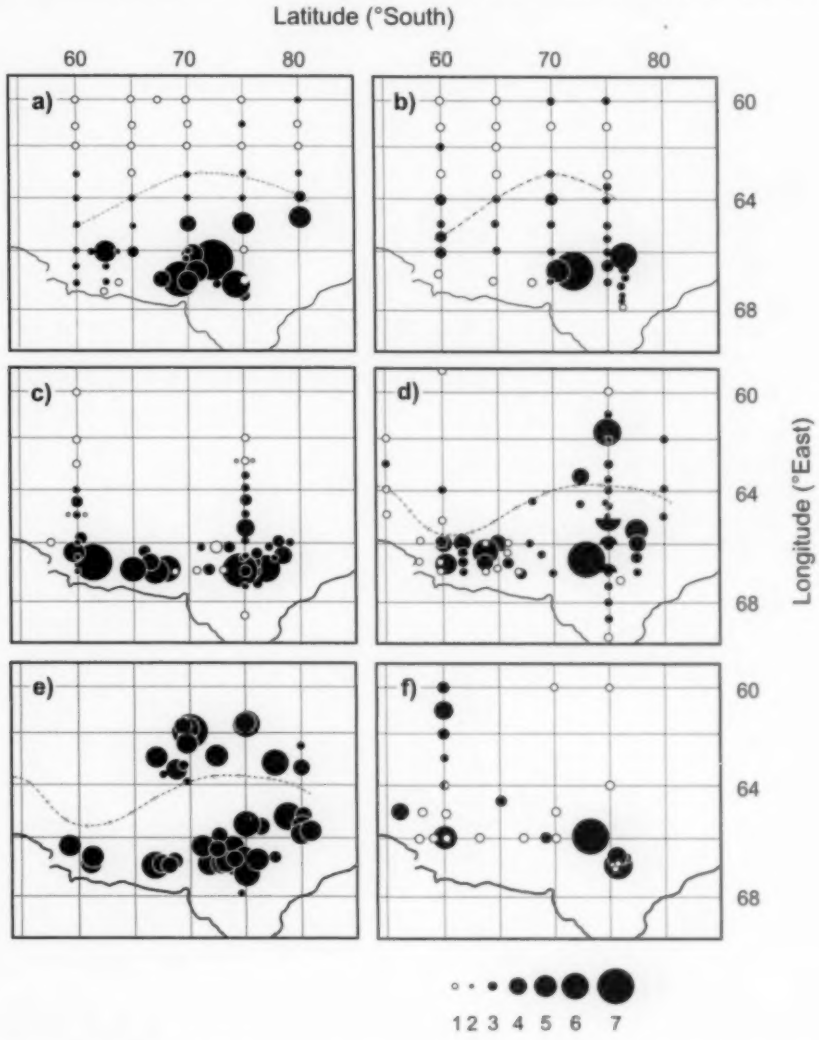
Fig. 5. Spatial distribution of Antarctic krill biomass in the Cooperation Sea from net sampling (modified from Pakhomov 1991). (*a*) 1985, oblique tows; (*b*) 1986, obliques tows; (*c*) 1987, oblique tows; (*d*) 1988, oblique tows; (*e*) 1988, target tows; (*f*) 1989, oblique tows. Biomass (g wet weight·1000 m^{-3}): 1, no krill; 2, <5; 3, 5–20; 4, 21–50; 5, 51–100; 6, 101–250; 7, >250.



with the largest estimates of average krill biomass density obtained in 1977 and 1990 (Fig. 7). Slightly elevated biomass densities were also observed during 1984 and 1986. Intercomparisons between krill biomass dynamics in the northern and southern parts of the Cooperation Sea were generally similar (Fig. 7).

Reproduction: breeding season, breeding locations, and larvae distribution

According to the development stage composition of adult krill and the age distribution of krill larvae observed during January–March in the Cooperation Sea, spawning persists from December to April (Menshenina et al. 1988; Hosie 1991; Samyshev 1991). In the southern part of the Cooperation Sea, it is most intense in late December and January (Pinchukov and Pakhomov 1987; Pakhomov and Karpenko 1988, 1992). During January, females at the spawning phase range between 30 and 40% of the total population (Pinchukov and Pakhomov 1987; Miquel 1991; Pakhomov and Karpenko 1992), whereas observations in the region during February and March revealed very low numbers of females (generally <5%) ready for spawning (Samyshev 1991; Pakhomov 1995).

The spatial distribution of the spawning stock of the Antarctic krill population during all years of research has clearly indicated that breeding takes place in the oceanic waters over deepwater zones (Hosie et al. 1988; Miquel 1991; Pakhomov and Karpenko 1992). In the coastal regions, despite high krill biomass, the number of spawning specimens is negligible (Samyshev 1991). Detailed cluster analysis of the spatiotemporal changes in the length–frequency distribution and reproductive state of Antarctic krill during austral

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Fig. 6. Spatial distribution of Antarctic krill biomass in the Cosmonaut Sea from oblique net tows (modified from Pakhomov 1991). (*a*) 1987; (*b*) 1988; (*c*) 1989. Biomass (g wet weight·1000 m^{-3}): 1, no krill; 2, <5; 3, 5–20; 4, 21–50; 5, 51–100; 6, 101–250; 7, >250.

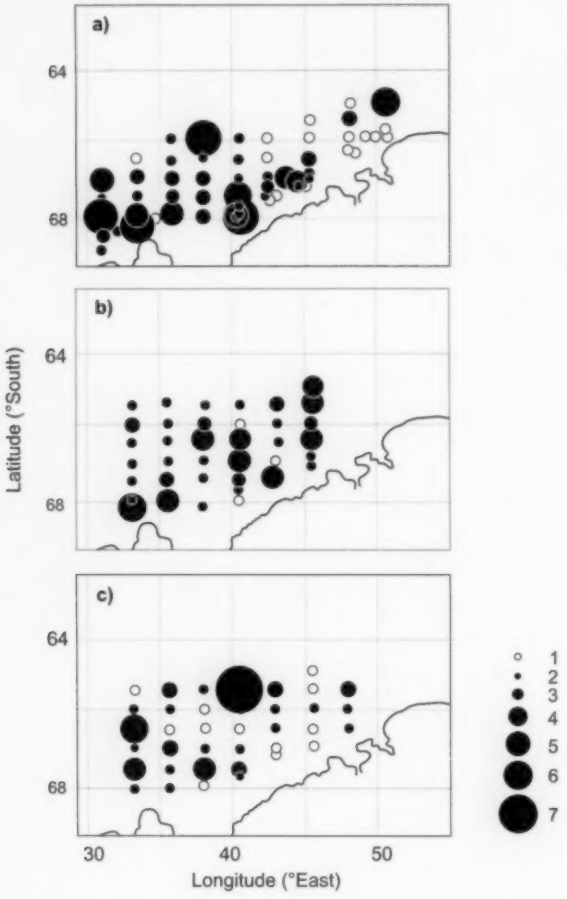
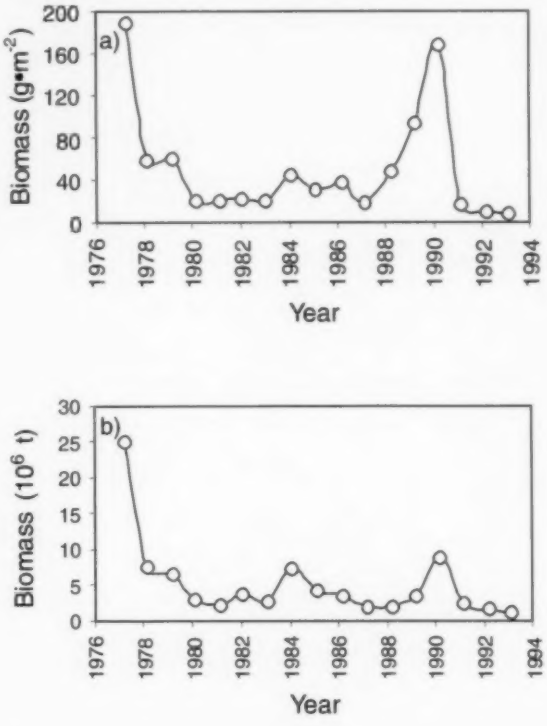


Fig. 7. Long-term variability in Antarctic krill biomass in the coastal region of the Cooperation Sea. Data (see values marked with an asterisk in Table 2) extracted from Shirakihara et al. (1986), Bibik and Yakovlev (1991), Samyshev (1991), and Pauly and Higginbottom (1994). On occasions when two independent estimates were obtained (1978, 1984, and 1985), an average value was used.



summer 1989 revealed a tight association of the krill life cycle with the major cyclonic circulation pattern south of the AD (Bibik et al. 1990). The smallest and the least mature specimens were observed in the southern central part of the Cooperation Sea, while the largest and most mature krill were found in the northern branch of the cyclonic circulation. In the western part of the circulation, a transitional situation has been identified, while in the eastern part of the region, large, often spent animals predominated (Bibik et al. 1990). This study thus suggests that the stationary cyclonic circulation in the central part of the Cooperation Sea may act as an nursery ground for the Prydz Bay region krill stock (Bibik et al. 1990).

Larvae of the calyptopis stage are mostly found in the coastal region of the western part of the Cooperation Sea (Hosie 1991; Samyshev 1991; Pakhomov and Karpenko 1992). These findings have led to the conclusion that oceanic spawning is unsuccessful and that larval recruitment is only possible from spawning occurring over the shelf region (Samyshev 1991). However, this does not take into account macroscale peculiarities of the deepwater circulation in the region south of the AD (Pakhomov and Karpenko 1992). In fact, eggs released in the oceanic region hatch in the warm deepwaters and are transported to surface waters (passive–active swimming) in a southward and northward direction by the movement of water in the AD region (Figs. 8 and 9). Here, they appear in the surface layer, where they are either concentrated in the nearshore region by mesoscale circulations or dispersed by surface currents (Hosie 1991; Pakhomov and Karpenko 1992).

The timing of reproduction in the region north of the AD in the Cosmonaut and Cooperation seas differs from the southern region. North of the AD, a substantial proportion (>20% of total) of females of the spawning stage are found throughout January–March, suggesting a prolonged spawning period probably with no definite peak (Bibik et al. 1988; Miquel 1991; Pakhomov 1995). The distribution of krill eggs indicates that spawning north of the AD does take place (Samyshev 1991). The fate of krill larvae in this area, particularly after they reach the surface, is, however, largely uncertain (Hosie 1991; Pakhomov and Karpenko 1992). Although enhanced densities of krill larvae have occasionally been observed north of the AD (Miller 1986; Miquel 1991;

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Table 1. Mean Antarctic krill abundance and biomass in the Cooperation and Cosmonaut seas estimated using different nets.

Period	Net	Sampling layer (m)	Abundance (individuals·1000 m^{-3})	Biomass (g wet weight·1000 m^{-3})	Source
Cooperation Sea					
Feb.–Mar. 1985	IK	0–52	214.8	95.69	Pakhomov 1991
Feb.–Mar. 1986	IK	0–66	23.0	16.8	Pakhomov 1991
Feb.–Mar. 1987	B	0–80	13.2	7.38	Pakhomov 1991
Feb.–Mar. 1987	IK	0–124	69.6	35.94	Pakhomov 1991
Dec.–Mar. 1987–1988	IK	0–150	139.9	58.73	Pakhomov 1991
Feb.–Mar. 1989	B	0–200	58.9	25.78	Pakhomov 1991
Mar.–Apr. 1984	B	0–150	No data	34.73	Miller 1986
Jan.–Feb. 1981	R	62–75	37.77	21.18	Hosie et al. 1988
Nov.–Dec. 1982	R	12–90	208.6	96.0	Hosie et al. 1988
Jan. 1984	R	Aimed	346.1	70.27	Hosie et al. 1988
Jan. 1985	R	0–200	5.94	2.03	Hosie et al. 1988
Jan. 1985	R	Aimed	190.9	170.2	Hosie et al. 1988
Jan.–Feb. 1985	R	0–150	3.31	3.12	Miquel 1991
Cosmonaut Sea					
Jan.–Feb. 1984	KT	0–150	No data	16.02	Bibik et al. 1988
Jan.–Feb. 1987	B	0–100	50.5	16.18	Pakhomov 1991
Jan.–Feb. 1987	IK	0–160	122.3	39.26	Pakhomov 1991
Feb. 1988	BMS	0–100	24.4	10.68	Pakhomov 1991
Feb. 1989	BMS	0–200	72.0	18.22	Pakhomov 1991
Mar.–Apr. 1989	B	0–200	16.4	4.81	Pakhomov 1991

Note: IK, Isaaks-Kidd trawl (6-m^2 mouth area, 5-mm mesh); B, Bongo net (0.5 m^2, 0.5 mm); R, RMT-8 (8 m^2, 5 mm); KT, krill trawl (30 m^2, 7 mm); BMS, Melnikov trawl (0.25 m^2, 0.5 mm); "aimed," specific horizontal tows made when krill swarms were located at a particular depth by ecosounder.

Fig. 8. Vertical distribution of sea temperatures, water movements, and Antarctic krill larvae (only maximum concentrations are shaded) along the 60 and 75°E transects in the Cooperation Sea during the summer seasons of 1985 and 1986 (modified from Pakhomov and Karpenko 1992).

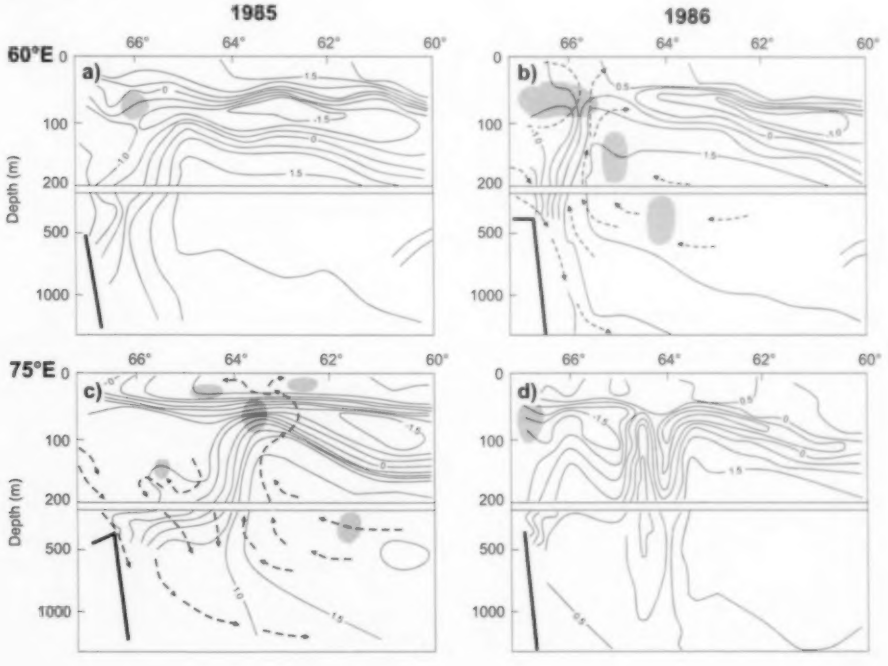

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Table 2. Mean and total Antarctic krill biomass in the Cooperation Sea.

Period	Area (km^2)	Mean biomass ($g \cdot m^{-2}$)	Total biomass (10^6 t)	Method	Source
Feb.–Mar. 1977	(1) 133 000	187.7*	25.0*	Trawls and acoustics	Samyshev 1991
	(2) 880 000	85.2	75.0		Samyshev 1991
	(3) 1 013 200	98.7	100.0		Samyshev 1991
Dec. 1977 – Jan. 1978	(1) 129 260	50.7*	6.555*		Samyshev 1991
	(2) 505 000	100.8	50.8		Samyshev 1991
	(3) 634 260	90.4	57.355		Samyshev 1991
Feb.–Mar. 1978	(1) 129 000	65.8*	8.487*		Samyshev 1991
	(2) 505 000	16.8	8.48		Samyshev 1991
	(3) 634 000	26.8	16.967		Samyshev 1991
Feb. 1979	(1) 107 600	60.7*	6.533*		Samyshev 1991
	(2) 673 000	27.1	18.23		Samyshev 1991
	(3) 780 600	31.7	24.763		Samyshev 1991
Jan. 1980	(1) 133 000	20.5*	2.72*		Samyshev 1991
	(2) 964 000	10.5	10.12		Samyshev 1991
	(3) 1 097 000	11.7	12.84		Samyshev 1991
Jan.–Mar. 1981	(1) 112 400	20.0*	2.25*		Samyshev 1991
	(2) 1 177 000	14.0	16.48		Samyshev 1991
	(3) 1 289400	14.5	18.73		Samyshev 1991
Dec. 1980 – Mar. 1981	(3) 1 280 000	1.25	1.6	Acoustics	Higginbottom et al. 1988
Dec. 1981 – Jan. 1982	(1) 168 000	22.6*	3.801*	Trawls and acoustics	Samyshev 1991
	(2) 673 000	12.7	8.55		Samyshev 1991
	(3) 841 000	14.7	12.351		Samyshev 1991
Dec. 1982 – Jan. 1983	(1) 126 800	21.3*	2.697*		Samyshev 1991
	(2) 1 000 000	50.4	50.4		Samyshev 1991
	(3) 1 126 800	47.1	53.097		Samyshev 1991
Dec. 1983	(2) 171 000	14.3	2.44	Acoustics	Shirakihara et al. 1986
Dec. 1983 – Jan. 1984	(1) 124 000	71.0*	8.81*	Trawls and acoustics	Samyshev 1991
	(2) 669 000	24.2	12.3		Samyshev 1991
	(3) 793 000	26.6	21.11		Samyshev 1991
Jan.–Feb. 1984	(3) 1 280 000	2.73	3.5	Acoustics	Higginbottom et al. 1988
Jan.–Feb. 1984	(3) 345 000	17.5*	6.04*	Acoustics	Shirakihara et al. 1986
Mar.–Apr. 1984	(3) 66 457	8.3	0.55	Bongo net	Miller 1986
Jan.–Feb. 1985	(3) 620 000	0.5	0.289	RMT-8	Miquel 1991
Jan.–Feb. 1985	(3) 1 280 000	2.89	3.7	Acoustics	Higginbottom et al. 1988
Jan.–Feb. 1985	(1) 150 000	20.2*	3.02*	Trawls and acoustics	Higginbottom et al. 1988
Feb. 1985	(1) 123 000	41.1*	5.1*		Samyshev 1991
Feb. 1986	(1) 94 000	36.6*	3.44*		Samyshev 1991
Feb. 1987	(1) 105 000	18.3*	1.92*		Samyshev 1991
Feb.–Mar. 1988	(1) 42 000	48.0*	2.0*	Acoustics	Bibik and Yakovlev 1991
Feb. 1989	(3) 540 000	22.0	12.0		Bibik and Yakovlev 1991
Mar. 1989	(1) 37 800	92.0*	3.5*		Bibik and Yakovlev 1991
Jan. 1990	(3) 590 000	47.0	28.0		Bibik and Yakovlev 1991
Feb.–Mar. 1990	(1) 53 800	167.0*	9.0*		Bibik and Yakovlev 1991
Jan.–Feb. 1991	(1) 150 000	16.7*	2.47*	Acoustics	Pauly and Higginbottom 1994
Feb.–Mar. 1992	(1) 150 000	10.3*	1.53*		Pauly and Higginbottom 1994
Jan.–Feb. 1993	(1) 150 000	7.7*	1.15*		Pauly and Higginbottom 1994

Note: Numbers in parentheses: 1, coastal region (south of 65°30′S); 2, oceanic region (between 60 and 65°30′S); 3, total region (south of 60°S). Astertisks indicate krill biomass estimates used in Fig. 7.

Pakhomov and Karpenko 1992), their concentrations were generally low. This might be a reflection of the prolonged spawning period and unfavorable feeding conditions. Nevertheless, during June 1973, krill larvae mainly at the calyptopis III – furcilia I stage were caught in large numbers (up to 3850 individuals·m^{-2}, average 22 individuals·m^{-2}, 0–100 m) within the anticyclonic circulation between 30 and 55°E and between 60 and 64°S (Aseev and Rubinshtein 1983). This provides some evidence that oceanic spawning may, indeed, at times be successful.

Observations of the distribution and abundance of krill larvae over the period 1978–1989 have indicated alternate years of low (1980 and 1983), medium (1978, 1982, 1984, 1988, and 1989), and high (1979, 1981, 1985, 1986, and 1987) spawning success (Pakhomov and Koltsov 1987; Menshenina et al. 1988; Samyshev 1991). However, there is

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Fig. 9. Generalized diagram of Antarctic krill spawning in the Cooperation Sea based on larval distribution patterns presented in Samyshev (1991) and Pakhomov and Karpenko (1992). 1, regions of larval accumulation; 2, regions of krill spawning stock accumulation.

only a weak relationship between spawning success and krill biomass (Samyshev 1991). Spatially, calyptopis larvae were found throughout the whole region south of 59°S in 1978, 1979, 1984, and 1985 and partially in 1980, while only nearshore concentrations of larvae were observed during 1981, 1983, and 1986–1989 (Samyshev 1991, 1993; Pakhomov and Karpenko 1992). Larval dispersal has been found to be closely correlated with the surface currents (Hosie 1991). These data suggest that calyptopis larvae are either transported in a westerly direction or are advected north and northeast of the Prydz Bay region. The survival of the latter larvae seems doubtful, as food concentrations have been found to be insufficient for their successful growth and survival (Hosie 1991). Whether these krill larvae could be returned to the Prydz Bay region by the eastern return branches of the Prydz Bay region gyre or perish is unknown. There are, however, some indications of southward advection/drift of krill in the eastern part of the Cooperation Sea (Samyshev 1991), which suggests that such a transport may exist.

Size/age composition and distribution

As demonstrated by studies conducted in the region off the Antarctic Peninsula (Siegel et al. 1997), a clear spatial segregation of the krill size groups has also been observed during austral summer in the central part of the Indian sector of the Southern Ocean. The smallest size groups were generally recorded in the coastal region, while the largest specimens dominated catches in the northern regions of both the Cosmonaut and Cooperation seas (Aseev 1983; Aseev et al. 1988; Miquel 1991). As a consequence, during most of the years of investigation, the size/age composition in the regions north and south of the AD was substantially different (Pakhomov 1995).

In the catches conducted between 1977 and 1990 in the Cooperation Sea, individual krill length ranged from 9 to 63 mm in the southern region and from 16 to 62 mm in the northern region (Tables 3 and 4). Similarly, in the Cosmonaut Sea, individual krill length ranged from 18 to 60 mm south of the AD and from 26 to 64 mm north of the AD (Table 5). Several studies conducted in different sectors of the Southern Ocean have concluded that Antarctic krill live for at least 5–6 years (Ivanov 1970; Aseev 1983; Siegel 1991) and may even live as long as 7–9 years (Ettershank 1984; Ikeda 1985; Rosenberg et al. 1986). Long-term observations in the Cooperation Sea showed that at least four age groups are identifiable in the region south of the AD, while five age groups were recorded in the region north of the AD (Fig. 10). If the larval stages are included, a life span of no less than 5 years for the southern groupings and 6 years for the northern groupings could be expected (Pakhomov 1995). The 5+ age group identified in the Cooperation Sea appears to be similar to the 4+ age group found in the northern part of the Cosmonaut Sea (see below). Therefore, in my opinion, the majority of the northern stock should also live for at least 5 years. In the Cosmonaut Sea, however, only four age groups (excluding larvae), corresponding to 5 years of life, have been distinguished in the curves of krill size distribution for the period 1984–1990 in both regions, e.g., south and north of the AD (Table 5) (Pakhomov 1995).

In the Cosmonaut Sea, the mean sizes of the 2+ to 4+ age groups identified north of the AD were between 1 and 8 mm larger ($P < 0.05$) than those of the corresponding age groups in the south of the AD. This indicates that krill groups with different demographic parameters were sampled north and south of the AD in the Cosmonaut Sea (Pakhomov 1995). Conversely, the mean sizes of the four first age groups identified south and north of the AD in the Cooperation Sea were similar (Tables 3 and 4). The fifth age group was only clearly separated during some years in the northern region, where its contribution to the total population ranged from 7.4 to 9.5% in 1985 and in 1986 and was as high as 15% in 1990 (Fig. 10). The average size of the 5+ age group varied

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Table 3. Mean (±SD) Antarctic krill length (mm) of various age groups from the southern part of the Cooperation Sea calculated by mixture analysis (Macdonald and Pitcher 1979).

Period	Age group 1+	2+	3+	4+	Size range (mm)	No. of individuals	χ^2	df	Source
Mar. 1977	25.9±2.85	37.1±3.91	45.2±3.27	51.9±2.15	20–57	2413	3.59	11	Aseev et al. 1988
Mar. 1978	26.0±1.20	35.9±5.09	46.9±3.79	52.9±1.17	23–58	1595	1.74	10	Aseev et al. 1988
Jan.–Feb. 1979	—	—	46.3±3.10	51.0±2.76	36–59	8849	1.02	7	Aseev et al. 1988
Mar. 1980	—	35.5±4.10	45.1±3.10	—	23–52	619	1.35	10	Aseev et al. 1988
Feb. 1981	27.6±3.51	—	44.3±4.12	51.7±3.25	20–58	2227	2.73	12	Aseev et al. 1988
Feb. 1981 (oblique)	28.0±3.09	—	46.3±4.00	—	16–60	37.8*	1.47	17	Hosie et al. 1988
Feb. 1981 (aimed)	30.8±4.23	40.9±2.62	48.2±2.43	54.9±1.27	18–58	92.6*	0.63	10	Hosie et al. 1988
Jan. 1982	—	36.0±1.13	47.6±3.61	—	32–58	3867	3.54	9	Aseev et al. 1988
Dec. 1982	19.1±2.59	35.5±4.29	48.8±3.21	—	18–58	208.6*	5.01	17	Hosie et al. 1988
Jan. 1983	22.8±3.49	—	41.3±4.81	50.2±4.08	15–60	3231	1.67	14	Aseev et al. 1988
Jan.–Feb. 1983	22.2±3.12	—	41.2±5.04	51.3±4.45	14–61	1856	11.9	23	Samyshev 1991
Jan.–Feb. 1984	23.0±3.03	32.0±3.11	40.0±5.42	47.5±3.74	16–57	4889	11.2	22	Samyshev 1991
Jan. 1984	19.0±2.84	34.3±3.14	42.3±3.94	—	14–58	346.1*	7.24	14	Hosie et al. 1988
Jan.–Feb. 1984	22.0±3.26	36.7±3.42	43.5±2.81	50.0±2.86	16–61	1238	3.20	18	Aseev et al. 1988
Mar.–Apr. 1984	19.5±2.12	33.9±2.46	43.1±2.87	51.5±2.99	15–59	2685	10.7	21	Miller 1986
Jan. 1985 (oblique)	21.2±2.40	39.4±6.40	—	51.1±2.19	14–58	5.94*	0.11	14	Hosie et al. 1988
Jan. 1985 (aimed)	—	40.0±5.52	45.0±4.03	—	12–58	190.9*	3.31	9	Hosie et al. 1988
Jan.–Feb. 1985	22.2±2.95	38.5±2.0	47.0±2.56	52.5±3.53	16–60	3.80*	0.31	21	Miquel 1991
Feb. 1985	26.8±4.75	36.3±2.80	44.8±3.35	51.0±3.37	15–60	2178	13.4	22	Pakhomov 1995
Dec. 1985–Jan. 1986	24.1±2.30	34.7±2.46	45.2±4.42	51.0±1.68	18–59	620	7.5	19	E.A. Pakhomov, unpublished data
Feb. 1986	—	31.0±3.00	40.5±4.20	48.9±3.20	22–60	1485	9.8	18	Pakhomov 1995
Feb. 1987	24.1±3.40	35.0±3.45	41.3±3.60	50.4±3.20	20–60	4085	12.6	18	Pakhomov 1995
Dec. 1987	19.8±3.04	—	43.7±4.85	51.1±1.10	16–54	206	6.9	19	E.A. Pakhomov, unpublished data
Jan. 1988	21.9±2.56	36.7±2.37	45.2±4.06	52.4±4.64	16–61	1924	4.22	22	E.A. Pakhomov, unpublished data
Feb. 1988	30.3±5.25	39.1±2.79	45.1±3.44	—	18–58	1134	14.3	19	Pakhomov 1995
Apr. 1988	—	34.9±4.47	46.8±2.01	51.6±2.91	28–60	71	6.7	16	E.A. Pakhomov, unpublished data
Feb. 1989	25.5±2.52	39.2±2.83	46.4±3.08	50.9±3.11	20–58	859	9.9	19	Pakhomov 1995
Mar. 1989	27.5±2.53	37.8±2.58	45.3±2.90	54.1±1.7	18–60	4462	8.18	20	E.A. Pakhomov, unpublished data
Jan. 1990	26.6±2.10	—	46.6±4.36	—	24–62	2327	12.1	20	E.A. Pakhomov, unpublished data
Feb. 1990	29.3±4.63	—	45.6±3.56	49.4±3.85	9–63	7139	16.0	27	Pakhomov 1995
Mar. 1990	26.5±2.20	37.9±2.37	44.8±2.94	50.9±2.08	22–56	1051	4.4	17	E.A. Pakhomov, unpublished data
Average	24.5±3.43	36.4±2.48	44.6±2.59	51.2±1.58					

Note: —, no age group was identified by mixture analysis; asterisks indicate average abundance (individuals·1000 m^{-3}); χ^2 describes the goodness-of-fit of the model to the data.

between 54.2 and 57.8 mm (Table 4) and was not significantly different ($P > 0.05$) from the average size of the 4+ age group identified in the northern part of the Cosmonaut Sea (Tables 4 and 5). The peculiar size/age composition identified in the northern Cosmonaut Sea and the periodic recording of the 5+ age group in the northern Cooperation Sea suggest that these animals do not belong to the southern krill stocks and are most likely advected from elsewhere (Pakhomov 1995). These data therefore confirm an earlier suggestion (Aseev et al. 1988) that krill from the Weddell Drift may reach the northern part of the Cosmonaut Sea and sometimes may be even advected into the northern part of the Cooperation Sea (Pakhomov 1995).

In the southern Cooperation Sea, remarkably large-sized krill (larger than the mean size of the 4+ age group) were collected (Pakhomov 1995). These specimens, however, did not exhibit distinct peaks in the length–frequency distribution and, as a consequence, could not be isolated using Macdonald and Pitcher's (1979) mixture analysis. Therefore, the existence of the 5+ age group in the region south of the AD cannot be conclusively proven. Previously, Aseev (1983) and Ettershank (1984, 1985), employing different techniques, suggested the presence of five adult year groups in the Prydz Bay region. It seems likely that even if the 5+ age group does persist in the southern part of the Cooperation Sea, its contribution to the total population is negligible (Hosie et al. 1988; Pakhomov 1995).

In the southern part of the Cooperation Sea, all four age

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Table 4. Mean (±SD) Arctic krill length (mm) of various age groups from the northern part of the Cooperation Sea calculated by mixture analysis (Macdonald and Pitcher 1979).

Period	Age group 1+	2+	3+	4+	5+	Size range (mm)	No. of individuals	χ^2	df	Source
Jan.–Feb. 1983	—	32.1±4.35	—	50.1±4.31	—	16–60	1127	12.9	24	Samyshev 1991
Jan.–Feb. 1984	23.3±3.91	37.2±4.79	47.7±3.28	53.5±3.68	—	16–60	7043	9.11	23	Samyshev 1991
Jan.–Feb. 1984	—	35.8±1.50	44.7±2.55	49.4±2.21	—	34–54	684	1.31	10	Aseev et al. 1988
Jan. 1985	—	32.9±5.07	—	49.1±3.43	—	24–58	402	4.02	18	Ikeda et al. 1986
Jan.–Feb. 1985	28.0±4.84	—	—	50.9±2.63	55.0±2.02	28–60	3.31*	0.17	16	Miquel 1991
Feb. 1985	29.9±2.47	—	—	49.9±3.17	57.7±1.29	28–61	454	9.0	17	Pakhomov 1995
Dec.1985 – Jan.1986	26.7±2.98	37.2±2.98	44.0±1.70	51.0±2.97	—	20–60	153	11.4	19	E.A. Pakhomov, unpublished data
Feb. 1986	29.0±2.10	35.0±3.10	41.1±3.30	49.8±3.29	54.2±3.20	27–62	391	6.5	13	Pakhomov 1995
Feb. 1987	—	—	39.3±2.87	51.9±3.34	—	32–60	280	7.6	14	Pakhomov 1995
Dec. 1987	23.7±3.85	30.5±2.08	40.3±4.30	48.9±3.20	—	12–60	4988	12.2	23	E.A. Pakhomov, unpublished data
Jan. 1988	23.6±2.13	37.2±2.33	—	46.6±3.90	—	18–58	363	11.6	20	Pakhomov 1995
Feb. 1989	28.0±2.10	34.8±2.51	43.2±3.00	49.5±3.10	—	23–60	1188	10.4	17	Pakhomov 1995
Jan. 1990	25.0±3.48	37.5±3.51	48.0±2.02	54.5±2.81	57.8±2.97	18–62	1359	6.26	22	E.A. Pakhomov, unpublished data
Feb. 1990	25.4±1.17	35.8±2.06	44.9±3.53	50.73.13	—	22–58	907	9.5	16	Pakhomov 1995
Apr. 1990	—	37.4±2.36	47.2±2.02	52.0±1.59	—	34–58	4655	3.25	12	E.A. Pakhomov, unpublished data
Average	26.3±2.41	35.3±2.33	44.0±3.09	50.5±1.94	56.2±1.85					

Note: —, no age group was identified by mixture analysis; the asterisk indicates average abundance (individuals·1000 m^{-3}); χ^2 describes the goodness-of-fit of the model to the data.

Table 5. Mean (±SD) Antarctic krill length (mm) of various age groups from the Cosmonaut Sea calculated by mixture analysis (Macdonald and Pitcher 1979).

Period	Age group 1+	2+	3+	4+	Size range (mm)	No. of individuals	χ^2	df	Source
South of the AD									
Jan.–Feb. 1984	—	35.6±2.92	41.0±3.67	—	28–51	424	2.80	12	Aseev et al. 1988
Jan.–Feb. 1987	27.4±3.15	37.8±3.25	42.3±3.48	—	20–58	1761	5.24	19	E.A. Pakhomov, unpublished data
Mar. 1987	28.0±2.70	37.5±4.37	48.3±3.15	—	20–60	800	10.2	18	Pakhomov 1995
Mar. 1988	30.6±2.12	—	44.1±4.01	—	24–56	563	10.7	17	Pakhomov 1995
Mar. 1989	25.7±3.01	32.8±3.15	40.9±4.28	49.2±2.96	18–54	296	9.5	16	Pakhomov 1995
Apr. 1989	25.2±1.97	34.2±3.50	44.1±2.82	—	22–54	1813	5.0	16	E.A. Pakhomov, unpublished data
Jan. 1990	26.4±0.72	37.9±2.21	43.6±1.16	—	22–58	1827	7.2	18	E.A. Pakhomov, unpublished data
Mar. 1990	29.0±3.50	37.0±3.01	42.5±3.50	52.0±4.00	20–56	2160	10.6	19	Pakhomov 1995
Average	27.5±1.91	36.1±1.99	44.0±2.68	50.6±1.98					
North of the AD									
Jan.–Feb. 1984	—	38.7±1.92	—	52.7±3.32	36–62	389	3.24	14	Aseev et al. 1988
Apr. 1989	27.8±3.80	40.7±3.30	49.3±3.51	55.0±2.32	26–64	307	11.7	18	Pakhomov 1995
Average	27.8	39.7±1.44	49.3	53.9±1.63					

Note: —, no age group was identified by mixture analysis; χ^2 describes the goodness-of-fit of the model to the data.

groups were clearly represented in the catches throughout the period 1977–1990. Although the first age group was generally poorly represented (Fig. 10), there were exceptions when this age group numerically contributed up to 30–40% of the total krill abundance (e.g., February 1981, January 1985, December 1987) (Fig. 10). Over the 14-year period, there were several abundant generations of krill, hatched in 1975, 1978, 1980, 1982, and 1984–1987 (Fig. 10). Interestingly, with only one exception (1980), these generations coincided with the years of high and medium spawning success (see above). Unlike the southern group, the age distribution in the northern Cooperation Sea, with only four exceptions, was generally dominated by the 4+ age group and occasionally by the 3+ age group (Fig. 10). The excep-

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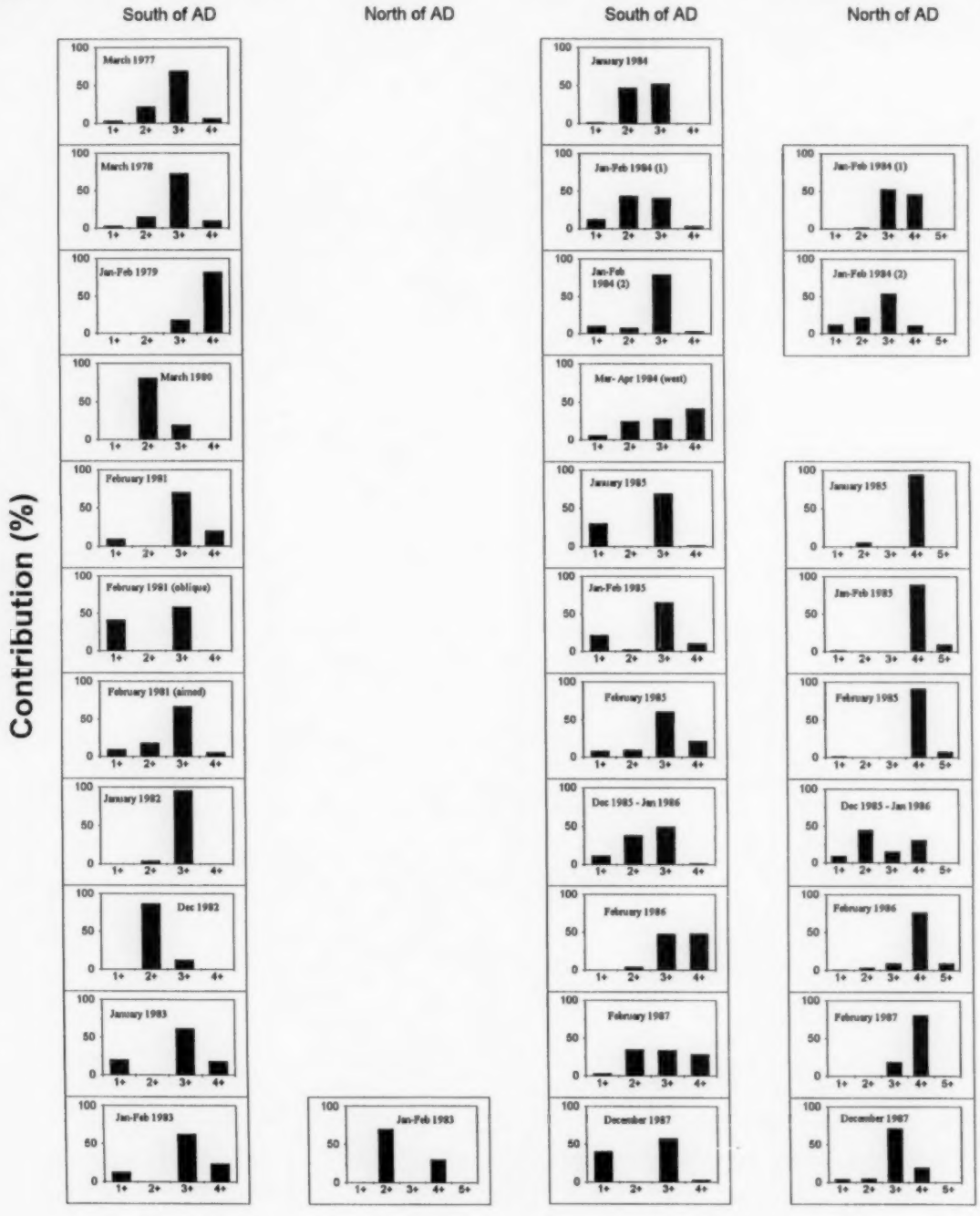
Fig. 10. Age distribution of Antarctic krill in the southern and northern parts of the Cooperation Sea during the summer seasons of 1977–1990.



tions were January–February 1983 and December 1985 – January 1986 when the contribution of the 2+ age group was the highest and January–February 1984 and January 1990 when the contribution of the two first age groups was substantial (Fig. 10). In addition, the generations hatched in 1981 (first appeared in January–February 1983) and in 1984

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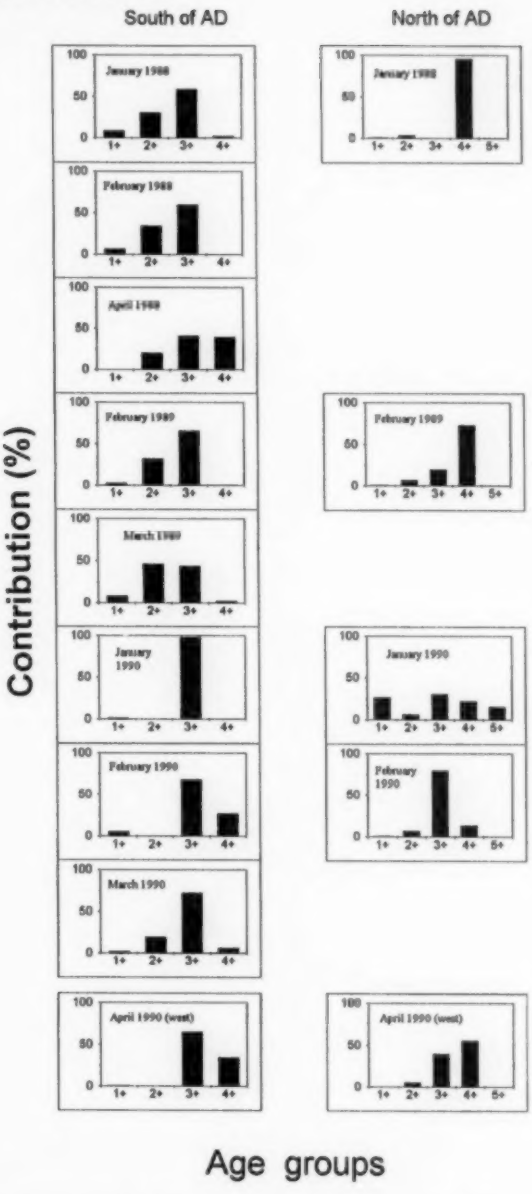
Fig. 10 (*concluded*).



(first appeared in December 1985 – January 1986) were traceable for at least 3 years (Fig. 10). Intercomparison between age composition dynamics in the southern and northern regions indicated that the 1981 generation, found north of the AD, was present south of the AD in 1984, while the 1984 generation was well represented throughout the entire Cooperation Sea during 1986–1988 (Fig. 10).

In the southern part of the Cosmonaut Sea, although all four age groups were encountered between 1984 and 1990, the 4+ age group was always poorly represented (Fig. 11). This could reflect net avoidance due to the sampling technique employed during these surveys (Table 1). Age composition in January–February 1984 was dominated by the two cohorts hatched in 1981 and 1982. Between 1987 and 1990, two cohorts (krill hatched in 1985 and 1987) were clearly identified over at least 2 or 3 consecutive years (Fig. 11). In January–February 1987, the cohort hatched in 1984 was also well represented (Fig. 11). Similar to the Cooperation Sea, in the northern part of the Cosmonaut Sea, only the 3+ (April 1989) and 4+ (January–February 1984) age groups dominated krill age composition (Fig. 11). In this small data set, there was no coincidence between age composition of krill in the regions south and north of the AD aside from the fact that missing age groups from the southern region were well represented in the northern part of the Cosmonaut Sea (Fig. 11).

It is worth noting that the krill age dynamics in the southern parts of the Cooperation and Cosmonaut seas during 1984 and between 1987 and 1990 were almost identical, suggesting a strong link between these two regions (Figs. 10 and 11). Furthermore, the abundant 3+ age group identified in the northern part of the Cosmonaut Sea during April 1989 is likely to have contributed to the relatively abundant 5+ age group in the northern part of the Cooperation Sea in 1990 (Figs. 10 and 11). The above-mentioned similarities provide evidence for the substantial exchange between these regions and are in agreement with the general circulation pattern discussed previously.

Recruitment

The recruitment indices R_1 and R_2 calculated from the age composition data in the Cooperation and Cosmonaut seas using the approach described by de la Mare (1994) are presented in Tables 6 and 7. The proportion of recruits (R_1 and R_2) is the ratio of numbers in the first and second age-classes to the numbers of all age-classes combined (de la Mare 1994). The R_1 and R_2 values should be treated with caution because much of the data employed to calculate recruitment indices were not presented in the form of haul-by-haul densities by length-class (de la Mare 1994). Despite these possible sources of error, there is a reasonable agreement between the R_1 and R_2 indices calculated here and those published in the literature for 1981, 1985, and 1987 (Table 6) (de la Mare 1994).

Recruitment indices R_1 and R_2 calculated for the 14-year period in the southern part of the Cooperation Sea ranged from 0 to 0.413 and from 0 to 0.868, respectively. Excluding all observations with zero values, the average R_1 value was 0.106 ($n = 27$) and the average R_2 value was 0.295 ($n = 21$). Our average R_1 index is therefore substantially lower than the average value of 0.219 ($n = 5$) calculated previously (de la Mare 1994). However, the average R_2 was similar to the value (0.252, $n = 6$) presented by the same author (de la Mare 1994). Our average recruitment indices are also comparable with values calculated using a long-term data set for the Atlantic sector of the Southern Ocean (Siegel and Loeb 1995; Siegel et al. 1997). In the southern part of the Cosmonaut Sea, the average R_1 value (0.146, $n = 7$), although higher than that calculated for the Cooperation Sea, was again lower than values obtained for the Indian and Atlantic sectors of the Southern Ocean. However, the average R_2 value (0.498, $n = 7$) was substantially higher than those reported for any other region of the Southern Ocean (de la Mare 1994; Siegel and Loeb 1995; Siegel et al. 1997).

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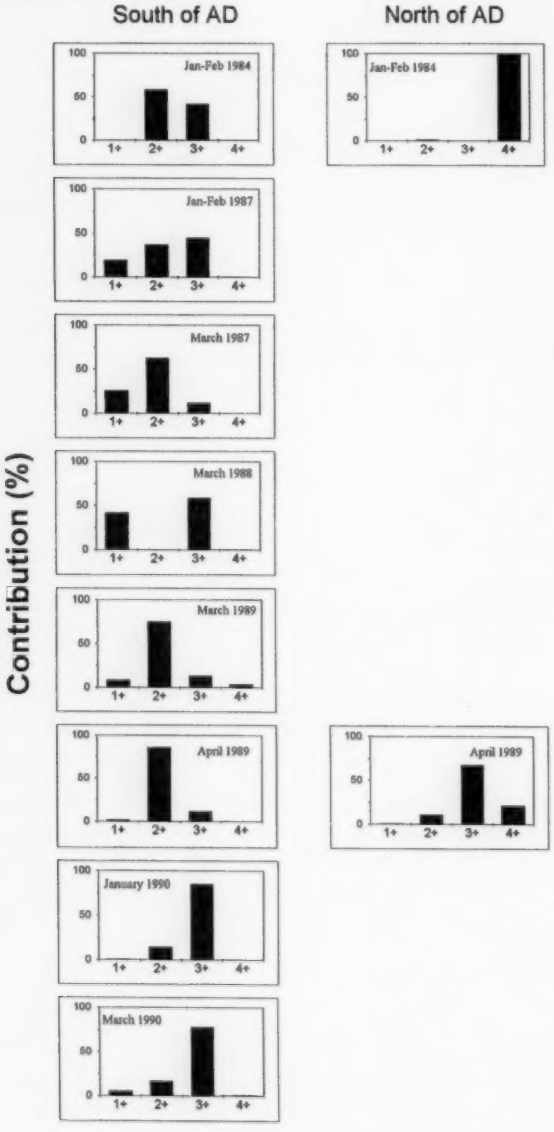
Fig. 11. Age distribution of Antarctic krill in the southern and northern parts of the Cosmonaut Sea during the summer seasons of 1984 and 1987–1990.



Despite similarities between average estimates, the recruitment index R_1 of the first age group in the southern parts of the Cosmonaut and Cooperation seas, with few exceptions, was remarkably low. A similar pattern was observed in the northern region of both seas. Unlike the R_1 indices, the R_2 recruitment index was always pronounced in the southern parts but much less prominent in the regions north of the AD. It is noteworthy that the R_2 values were generally higher than those of R_1 for the same year-class (Tables 6 and 7). Several explanations have been proposed to account for this discrepancy (de la Mare 1994; Siegel et al. 1997). Firstly, the 1+ age group may be undersampled by nets with large mesh size (4–5 mm) (Siegel 1986). This may be of particular relevance to this study, as samples were collected using nets with a mesh size of 5–7 mm, especially since the contribution of the 1+ age group was always elevated in the years when krill were collected using Bongo nets or nets with small mesh size (<1 mm) (Miller 1986, data collected in the southern part of the Cosmonaut Sea). Secondly, it is likely that the sampling strategy did not adequately address the vertical and horizontal patterns of distribution of the 1+ age group. For example, the 1+ age group was often well represented in samples collected in close proximity to sea ice, which is known as a nursery for juvenile krill (Kottmeier and Sullivan 1987; Hamner et al. 1989; Daly 1990). This was particularly evident at the beginning and towards the end of the summer season (Miller 1986; Miquel 1991). Also, oblique or target tows generally undersample the top 1–10 m of the water stratum, which in the Cooperation Sea during the austral summers has been identified as the main location of juvenile krill with a modal size of 18 mm (Fig. 12) (Miller 1986; Krakatitsa et al. 1993). Thirdly, this bias could be associated with the distribution mixture technique (Siegel et al. 1997). Finally, environmental parameters, such as currents and meanders, may influence the various age groups differently. For example, in our data sets, specimens belonging to the 1+ age group were found most frequently in the southern region of both seas, where concentration by prevailing currents is more likely.

Interannual differences in R_1 in the southern part of the Cooperation Sea reflect highly variable year-class success. Recruitment anomalies revealed high and medium recruitment in 1981, 1983, 1985, 1988, and 1991 (Fig. 13). Anomalies in R_2 revealed the appropriate succession of the 1981 and 1988 as years of high recruitment, while it was not as obvious for 1983 and 1985. High recruitment of the 2+ age group occurred during 1991, while in 1990 the contribution of the 1+ age group was well bellow average. In the Cosmonaut Sea, R_1 was highest during 1988 and subsequently reflected by the highest R_2 indices from surveys conducted during the austral summer of 1989 (Table 7).

Growth, longevity, and mortality

Growth curves calculated during previous studies in the southern and northern parts of both the Cosmonaut and Cooperation seas are in very close agreement with each other and with the curves calculated for krill from the Bransfield Strait and Weddell Sea (Siegel 1987; Hosie et al. 1988; Pakhomov 1995). These curves provide evidence in support of the theoretical curve of Ikeda (1985), which proposes a growth period of 6 months with no growth during the winter (Hosie et al. 1988). Ikeda's (1985) curve proposed a total life span of Antarctic krill of 7.5 years. Siegel (1986) suggested that the maximum life span of krill in the Bransfield Strait is 5.3 years. The maximum life span of krill in the southern and northern parts of the central part of the Indian sector in the Cooperation and Cosmonaut seas was calculated as 5.8 and 5.6 years, respectively (Pakhomov

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Table 6. Antarctic krill year-class recruitment indices R_1 and R_2 in the Cooperation Sea from 1977 to 1993.

	South of the AD		North of the AD	
Period	R_1	R_2	R_1	R_2
Mar. 1977	0.032	0.219		
Mar. 1978	0.025	0.150		
Jan.–Feb. 1979	0.000	0.000		
Mar. 1980	0.000	0.806		
Feb. 1981	0.095	0.000		
Feb. 1981 (oblique)	0.413	0.000		
Feb. 1981 (aimed)	0.093	0.184		
Jan. 1982	0.000	0.043		
Dec. 1982	0.002	0.868		
Jan. 1983	0.203	0.000		
Jan.–Feb. 1983	0.129	0.000	0.000	0.703
Jan. 1984	0.015	0.466		
Jan.–Feb. 1984 (1)	0.122	0.437	0.000	0.017
Jan.–Feb. 1984 (2)	0.102	0.073	0.123	0.225
Mar.–Apr. 1984 (west)	0.059	0.247		
Jan. 1985 (oblique)	0.302	0.000	0.000	0.055
Jan.–Feb. 1985	0.211	0.023	0.011	0.000
Feb. 1985	0.078	0.095	0.013	0.000
Dec. 1985 – Jan. 1986	0.111	0.381	0.095	0.445
Feb. 1986	0.000	0.043	0.009	0.035
Feb. 1987	0.026	0.348	0.000	0.000
Dec. 1987	0.400	0.000	0.041	0.047
Jan. 1988	0.089	0.299	0.009	0.034
Feb. 1988	0.069	0.339		
Apr. 1988	0.000	0.200		
Feb. 1989	0.026	0.321	0.009	0.069
Mar. 1989	0.083	0.460		
Jan. 1990	0.015	0.000	0.261	0.063
Feb. 1990	0.052	0.000	0.007	0.068
Mar. 1990	0.022	0.194		
Apr. 1990 (west)	0.006	0.000	0.000	0.053
Jan.–Feb. 1981*	0.000	0.286		
Jan.–Mar. 1981*	0.167	0.096		
Jan.–Feb. 1985*	0.528	0.320		
Feb.–Apr. 1987*	0.025	0.231		
Jan.–Feb. 1991*	0.314	0.556		
Jan.–Feb. 1993*	0.064	0.020		

Note: Numbers in parentheses: 1, Aseev et al. (1988); 2, Samyshev (1991). Asterisks indicate recruitment indices calculated by de la Mare (1994).

Table 7. Antarctic krill year-class recruitment indices R_1 and R_2 in the Cosmonaut Sea from 1984 to 1990.

	South of the AD		North of the AD	
Period	R_1	R_2	R_1	R_2
Jan.–Feb. 1984	0.000	0.582	0.00	00.011
Jan.–Feb. 1987	0.192	0.363		
Mar. 1987	0.258	0.625		
Mar. 1988	0.417	0.000		
Mar. 1989	0.083	0.750		
Apr. 1989	0.020	0.862	0.008	0.108
Jan. 1990	0.005	0.139		
Mar. 1990	0.049	0.164		

Fig. 12. Length–frequency distribution of Antarctic krill in the top 1-m layer in the Cooperation Sea (modified from Krakatitsa et al. 1993).

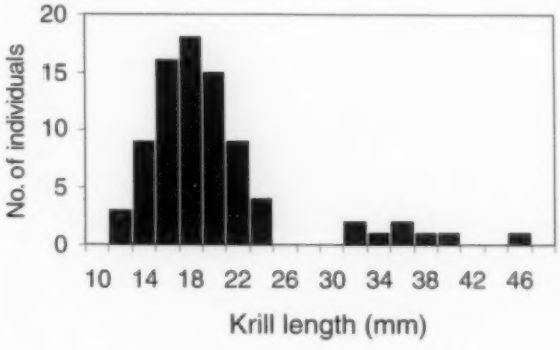
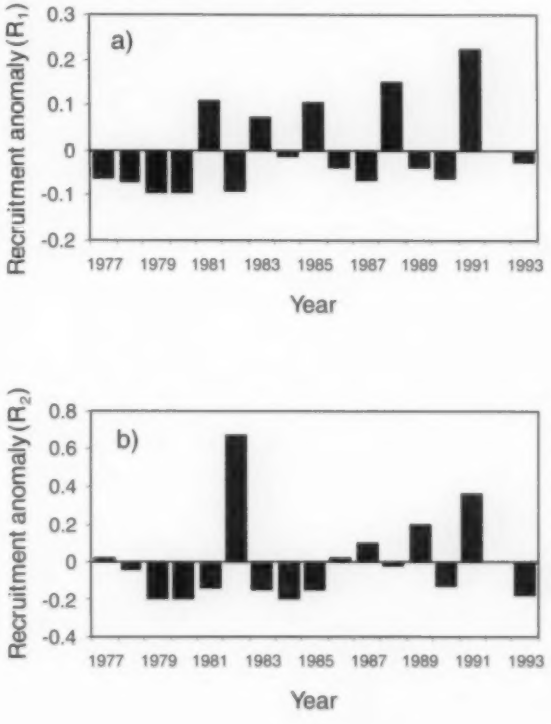


Fig. 13. Recruitment index anomalies in the southern part of the Cooperation Sea between 1977 and 1993.



1995). Discrepancies between our data and the theoretical curve of Ikeda (1985) suggest that we are missing at least two year-classes, which, as discussed above, could not be conclusively separated by the mixture analysis (Hosie et al. 1988; Pakhomov 1995). Antarctic krill mature in the Cooperation and Cosmonaut seas during their third year. Thus, unlike in the Atlantic sector (Bransfield Strait), where three mature age groups are present, in the Indian sector, there are only two mature age groups spawning (Ivanov 1970; Hosie et al. 1988; Pakhomov 1995). This is similar to the situation

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found in the Weddell Sea (Siegel 1987), indicating a lower spawning potential of krill stocks in the central part of the Indian sector of the Southern Ocean (Hosie et al. 1988).

Despite similar longevity, krill growth performance (k) in the Cooperation Sea and southern part of the Cosmonaut Sea, varying between 0.44 and 0.47, was higher than the values calculated (k = 0.42) for krill from the northern part of the Cosmonaut Sea (Pakhomov 1995). As a consequence, the time at which 50% of the asymptotic length is attained ($t_{50\%} = 0.693/k + t_0$; Siegel 1987) was slightly lower (1.48–1.53 years) for the southern groups in both seas and for the northern group in the Cooperation Sea than that calculated (1.56 years) for the northern group in the Cosmonaut Sea (Pakhomov 1995). This indicates a higher growth performance for Antarctic krill inhabiting the southern parts of the area investigated. This may suggest that different krill stocks exist in the Cooperation Sea and southern part of the Cosmonaut Sea and in the northern part of the Cosmonaut Sea (Pakhomov 1995).

The krill age-averaged natural mortality rates in the Cooperation and Cosmonaut seas, estimated using standard methods (e.g., Beverton and Holt 1956; Alverson and Carney 1975; Richter and Efanov 1977), varied considerably between 0.52 and 2.92 (Pakhomov 1995). The lowest values (0.52–0.57) were obtained using Richter and Efanov's (1977) equation, which takes into account the age at which 70% of individuals mature for the first time (Babajan et al. 1984). Intermediate mortality rates (0.72–0.87) were calculated employing Alverson and Carney's (1975) model, which considers the age at which the biomass peak of a population is reached. The most variable and highest mortality rates (0.76–2.92) were obtained following Beverton and Holt's (1956) approach, which is based on the natural krill length–frequency distributions. The last approach assumes that the population is fully represented in the catches, which was not always the case in the southern parts of both the Cosmonaut and Cooperation seas (see above). Indeed, mortality rates estimated using the Beverton and Holt's (1956) equation were consistently higher in the regions north of the AD and were probably most accurate for the older age groups (Pakhomov 1995).

The age-dependent natural mortality rates obtained with the Zikov and Slepokurov (1982) approach ranged from 0.52 during the maturation period to 1.1–2.41 during the first and last years of life (Pakhomov 1995). Interestingly, age-averaged mortality rates estimated using Alverson and Carney's (1975) and Richter and Efanov's (1977) methods were similar to the age-dependent mortality rates during the maturation period (probably due to similar assumptions considered), while mortality rates calculated with Beverton and Holt's (1956) approach corresponded well to the age-dependent mortality rates during the last years of life (Pakhomov 1995). A critical analysis of previous estimates of mortality rates, which has been discussed by Miller and Hampton (1989) and Siegel (1991), revealed that mortality rates range from 0.45 to 5.5. However, realistic values of age-averaged natural mortality may range from 0.66 to 1.35 (Siegel 1986, 1991; Priddle et al. 1988). Assuming that the longevity of animals is the age at which 99% of individuals die ($M_{1\%} = -\ln(0.01)/T = 4.605/T$; Alagaraja 1984), mortality would vary between 0.74 and 0.82 (Siegel 1991).

Stock identity

The population structure of Antarctic krill is still poorly understood (Miller and Hampton 1989; Knox 1994). It has been suggested that in areas of steady, cyclonic water circulations around the Antarctic continent (Treshnikov 1964), different and perhaps self-maintaining krill stocks may occur (Makarov 1972; Maslennikov 1980; Maslennikov and Solyankin 1980). Data on the distribution of krill larvae, on the interannual fluctuations in krill size/age composition, and on the infection by protozoan parasites (i.e., gregarines) allowed Dolzhenkov et al. (1987) to postulate a general model of krill population structure and movement across the Southern Ocean. The model suggests the co-occurrence of one simple and one more complex population of Antarctic krill around the Antarctic continent. The first population appeared to inhabit the eastern part of the Indian sector of the Southern Ocean (Mawson and Dumont D'Urville seas), while the second population, which was distributed throughout the rest of the remaining area of the Southern Ocean, consisted of at least four subpopulations. These would inhabit the Weddell Sea, the Riiser-Larsen and Cosmonaut seas, the Cooperation and Davis seas, and the Somov and Ross seas (Dolzhenkov et al. 1987). From the analyses of the size–frequency distribution of Antarctic krill, Latogursky et al. (1990) concluded that the reduction in the number of age groups in the northern parts of the eastern Antarctic supports the hypothesis that krill are advected from the west. Thus, it is likely that krill originating from the Weddell Drift may reach the Cosmonaut Sea (Aseev et al. 1988; Bibik et al. 1988; Latogursky et al. 1990) and, as has been shown in this study, may be traced during some years in the northern part of the Cooperation Sea. Latogursky et al. (1990) distinguished three major stocks of Antarctic krill, i.e., in the Weddell Sea, in the Bellingshausen Sea, and in the coastal region around the continent. However, biochemical and genetic data (Fevolden 1988; Fevolden and Schneppenheim 1989; Zane et al. 1998) concluded that a single, genetically homogeneous population of Antarctic krill occurs around the Antarctic continent. The presence of a single metapopulation could be explained by gene flow between the major areas of krill distribution facilitated by the main Southern Ocean currents. In the Cooperation Sea, neither latitudinal nor meridional significant genetic differences in krill have been found (Truveller et al. 1983; MacDonald et al. 1986; Fevolden 1988). However, krill samples collected by Russian expeditions during the summer seasons prior to 1983 (Truveller et al. 1983) showed that the genetic heterogeneity within the southern and northern belts of krill distribution was lower than that found between them in both the Cosmonaut and Cooperation seas. Although these data are preliminary, it is worth noting that the most recent mtDNA analyses have also indicated some degree of isolation between the east Weddell and South Georgia groups, which are separated by a secondary frontal feature (Zane et al. 1998).

The question of the presence of a self-maintained krill stock inhabiting the Cooperation Sea and its relationships with similar stocks in the adjacent regions thus still remains unanswered. Results of the above synthesis clearly indicated long-term covariance between the dynamics of the krill age groups and krill spawning success in the southern part of the Cooperation Sea. The circulation pattern in the area (Bibik

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et al. 1988; Gerasimchuk and Lanin 1988; Solyankin 1993) was one of the main reasons why a self-maintained krill stock was postulated (Pakhomov 1995). The obvious similarity in demographic parameters between the southern and northern krill groupings in conjunction with the substantial reduction in the first age groups north of the AD suggests that the northern grouping is mainly supported by the southern group being mainly composed of expatriates from the southern region. This varies between years, as our data clearly indicate. During the period from 1977 to 1990, there were at least two periods (in 1983 and 1986) when expatriation was significant (Fig. 10) (also see Samyshev 1991). Nevertheless, the northern krill stock of the Cooperation Sea may also include intruders originating from the Weddell Drift (Pakhomov 1995). It seems most likely that the northern grouping is transported eastwards beyond the Cooperation Sea. There is also some indication that during some years, specimens of this grouping may also be recruited back into the southern stock in the eastern part of the Cooperation Sea (Samyshev 1991). The northern grouping found in the Cosmonaut Sea is most likely a remnant of the Weddell Drift, probably originating from the Weddell and Bellingshausen seas (Aseev et al. 1988). Finally, the degree of isolation between the coastal regions of the Cosmonaut and Cooperation seas seems to be very low, as the size/age composition dynamics between these regions were very similar (Pakhomov 1995; this study). Unfortunately, little is known about the exchange of krill between the Cooperation and Davis seas, although transport of larvae and juveniles through the East Wind Drift has been suggested (e.g., Hosie 1991; Lanin 1993). The length–frequency data of krill collected between 1978 and 1982 analyzed by Dolzhenkov et al. (1987) showed a close correlation in the Cooperation and Davis seas. This allowed Dolzhenkov et al. (1987) to hypothesize that either these regions are closely linked or the biological cycles in the krill stock of both seas are highly synchronized. A generalized circulation pattern, presented by Lubimova et al. (1985), showed the existence of a macroscale gyre covering both the Cooperation and Davis seas, providing support for the hypothesis proposed by Aseev (1983). According to Aseev (1983), krill may drift northward up to 60°S and then eastward and southeastward, contributing to the krill stocks of the Cooperation and Davis seas. Although this hypothesis is speculative, it could be supported by circulation patterns (see Lubimova et al. 1985), assuming an average speed of water calculated from iceberg drift (Tchernia and Jeannin 1984). Unlike the above situation, exchange of specimens between the Cooperation and Cosmonaut seas appears to be real (Pakhomov 1995). Therefore, although it has been postulated that a self-maintained krill stock persists in the Cooperation Sea, the periodic resultant gene flow via recruits from the other regions seems likely to prevent the establishment of a genetically endemic subpopulation of the Antarctic krill in this region (Pakhomov 1995).

Long-term krill stock variability: effect of environmental and demographic parameters

The long-term observations in the Cooperation Sea, particularly in the southern region, indicate large changes in the total krill stock and averaged krill densities between 1977 and 1993 (Table 2; Fig. 7). Although different techniques were employed to assess krill density during this period, the general pattern observed was low krill biomass in the southern part of the Cooperation Sea with two periods (in 1977–1978 and 1989–1990) of high krill biomass. Several hypotheses have been proposed to explain the long-term variability in krill biomass in the Cooperation Sea. Following is a brief overview of the two most compelling models available in the literature.

The long-term observations (between 1974 and 1986) on environmental parameters in the Cooperation Sea (south of 60°S) revealed a 3-year cyclicity in the advection of warm deep waters into the region (Lanin 1993). Years of intensive advection culminating in appreciable changes in the geostrophic circulation patterns coincided with the summer seasons of 1977, 1980–1981, and 1983–1984 (Lanin 1993). Krill length–frequency distribution analyses conducted by Aseev et al. (1988) in the southern part of the Cooperation Sea revealed a similar periodicity in the appearance of the first two age groups of krill in this area. Aseev et al. (1988) and Lanin (1993) suggested that this was the result of the mechanical transportation of krill into the southern region with subsequent accumulation within the coastal frontal region. It was suggested that krill were trapped in the Prydz Bay Gyre for a period of at least 2 years and that before the next advection occurred, these krill would have become extinct (Aseev et al. 1988; Aseev 1990). Although this hypothesis does not explain long-term krill stock variability, a number of other biological and environmental parameters, e.g., mesozooplankton and phytoplankton density and nutrient concentrations, have been found to show similar 3-year cyclicity in the Cooperation Sea (Lanin et al. 1987; Lanin 1993).

The second hypothesis suggested that the accumulation and dispersal of krill in the Cooperation Sea region are highly affected by the atmospheric circulation over this region (Samyshev 1991). Krill stock, average surface density, and the persistence of krill superaggregations south of the AD were negatively correlated with Wolf's number (number of sun spots). Correlation analysis conducted between the Wolf number data and atmospheric circulation over the Cooperation Sea revealed the persistence of increased meridional atmospheric circulation during years of high Wolf numbers (Samyshev et al. 1987). This was suggested to increase the meridional advection of the surface waters to the north, thus decreasing the spatial isolation of the southern region from the adjacent northern region. Associated with this shift was an increase in krill expatriation from the southern part of the Cooperation Sea. During years with decreased sun activity (low Wolf numbers), the opposite situation occurred (Samyshev 1991).

In order to produce a model for forecasting krill biomass, Bryantsev et al. (1990) analyzed krill stock variability and atmospheric and oceanographic environmental variables in the southern part of the Cooperation Sea. Significant correlations ($P < 0.05$) of the prevailing atmospheric circulation (meridional or zonal) during the summer season and peculiarities of the macroscale circulation patterns during the same season with krill stock increase during the following year were found. These findings confirm the importance of atmospheric circulation in maintaining the spatial isolation

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Table 8. Variables used in correlation analyses.

Variable	Valid *n*	Source(s)
Antarctic krill biomass (g wet weight·m^{-2})	17	Bibik and Yakovlev 1991; Samyshev 1991; Pauly and Higginbottom 1994
Krill biomass (10^6 t)	17	Bibik and Yakovlev 1991; Samyshev 1991; Pauly and Higginbottom 1994
R_1	16	Table 6; de la Mare 1994
R_2	16	Table 6; de la Mare 1994
Deepwater input to the Cooperation Sea	11	Lanin 1993
Ice difference between December and September	24	www.antdiv.gov.au/science/glacio
Ice northmost position (September)	24	www.antdiv.gov.au/science/glacio
Ice southmost position (February)	24	www.antdiv.gov.au/science/glacio
Ice accumulation (difference between February and September)	23	www.antdiv.gov.au/science/glacio
Spawning success (larvae abundance)	11	Pakhomov and Koltsov 1987; Samyshev 1991, 1993
Average temperature at 100 m along 75°E between 60 and 67°S	14	E.A. Pakhomov, unpublished data
Salp abundance	10	Pakhomov 1991
Mesozooplankton abundance (0–100 m)	14	Savich 1993
Phytoplankton biomass (0–100 m)	11	Savich 1993
Wolf number	21	www.ngdc.noaa.gov/STP/SOLAR/SSN/SSN.html
Contribution of the 3+ and 4+ age groups (ranked)	15	Pakhomov 1995; E.A. Pakhomov, unpublished data

of this region and accumulative effect of the Prydz Bay Gyre, as previously suggested (Bryantsev et al. 1990). According to Samyshev (1991), the highest meridional atmospheric transport in 1983 coincided with the highest Wolf number during the previous year, and this was responsible for the advection of the first two age groups northward (also see Fig. 10). However, our data (Fig. 10) indicate that during the austral summer of 1986, a similar situation occurred, which is in contradiction with Samyshev's (1991) hypothesis. Independently, Pelevin (1987) showed that during the summer season of 1986, anomalous atmospheric circulation was observed over the Cooperation Sea. Unlike the normal situation where atmospheric transport in the eastward and westward directions dominates in the regions north and south of the AD, respectively, during the 1986 season, westward atmospheric transport predominated across the entire Cooperation Sea (Pelevin 1987). Pelevin (1987) postulated that in such a situation, the accumulation processes in the southern part of the Cooperation Sea would be substantially depressed and meridional krill advection would occur, which has subsequently been confirmed by size/age krill distribution dynamics (Fig. 10).

To further test the validity of the above hypotheses, a comprehensive correlation analysis including 16 variables (Table 8) collected in the Cooperation Sea was performed (Table 9). There were no meaningful correlations identified between krill biomass and any other biological or environmental parameter. However, krill biomass showed significant positive cross-correlation with the warm deepwater input into the area during the previous year. This suggests that high levels of deepwater input to the Cooperation Sea during the previous year results in an increase in krill biomass during next summer season. This concords with the first hypothesis, which suggested that during years of high water input, the first two age groups are passively concentrated and then trapped in the southern part of the Cooperation Sea. This process may be responsible for the predominance of the older age groups and the increase in krill biomass in the following year. Nevertheless, the only significant but very distant (lag –3) negative cross-correlation was obtained between krill biomass and the contribution of the 3+ and 4+ age groups. This association is most probably debatable in biological terms but may represent an artifact of the 3-year periodicity of biological parameters in the region (Aseev et al. 1988; Lanin 1993). Significant positive correlations between environmental variables also occur: between deepwater input to the Cooperation Sea, the southmost position of the ice, and ice accumulation during the following winter. From this, it is obvious that during years with high levels of deepwater input, the heat background of the Cooperation Sea is the greatest, which is consequently followed by the greatest ice accumulation the next winter. Notably, years of medium and highest deepwater input to the region of the Cooperation Sea coincide with the years of the earliest ice breakout dates at the Vestfold Hills (Whitehead et al. 1990).

High levels of deepwater input apparently promote favorable conditions for the survival of krill larvae ($r^2 = 0.8142$, $P < 0.05$). Although there was no correlation between deepwater input and the contribution of the 3+ and 4+ age groups to the total krill stock, the latter was positively correlated with spawning success ($r^2 = 0.6062$, $P < 0.05$), indicating the importance of these age groups in overall reproduction. The mean R_1 correlated negatively only with the ice position during September. This suggests that first-year recruitment was highest during the years of highest ice coverage of the Cooperation Sea. The mean R_2 was highly positively correlated with the average phytoplankton biomass during the same year and with the highest ice accumulation during the previous year. The above relationships indicate that ice conditions and food availability play an important role in the survival of the two age groups in the Cooperation Sea. There

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Table 9. Results of pairwise correlation and cross-correlation analyses between biological and environmental variables to show trends in association.

Pair of variables	Valid *n*	lag	r^2	*P*
R_1 and ice northmost position	16	0	–0.6417	<0.05
R_2 and phytoplankton biomass	11	0	0.8949	<0.005
R_2 and ice accumulation	11	1	0.7121	<0.05
Salp abundance and Wolf number	10	0	–0.6353	<0.05
Salp abundance and ice accumulation	10	0	0.8027	<0.005
Salp abundance and mesozooplankton abundance	10	0	–0.885	<0.05
Contribution of 3+ and 4+ groups and Wolf number	15	0	–0.6243	<0.05
Contribution of 3+ and 4+ groups and Spawning success	11	0	0.6062	<0.05
Spawning success and salp abundance	10	0	0.8299	<0.05
Spawning success and Wolf number	10	0	–0.679	<0.05
Mesozooplankton abundance and Wolf number	10	0	0.641	<0.05
Mesozooplankton abundance and ice southmost position	10	–1	0.7982	<0.05
Ice difference and ice accumulation	23	0	0.6964	<0.005
Ice northmost position and ice difference	24	0	–0.7215	<0.005
Deepwater input and ice accumulation	10	0	0.6418	<0.05
Deepwater input and spawning success	8	0	0.8142	<0.05
Deepwater input and ice southmost position	11	0	0.6776	<0.05
Deepwater input and ice difference	10	1	0.7256	<0.05
Ice southmost position and Wolf number	21	0	0.5268	<0.05
Ice northmost position and ice accumulation	23	0	–0.7879	<0.005
Antarctic krill biomass and deepwater input	10	1	0.6944	<0.05
Krill biomass and contribution 3+ and 4+ groups	10	–3	–0.8596	<0.05

were no meaningful correlations between the mean abundance of salps, krill biomass, and R_1 and R_2 values for the Cooperation Sea. Average salp abundances were, however, positively correlated with the ice accumulation during the following winter, indicating their predominance during the warmest years. Furthermore, salp abundance was positively correlated with spawning success, suggesting that during the years with high levels of deepwater input to the Cooperation Sea, salps are numerous. The years when salps were abundant were characterized by the lowest mesozooplankton abundance ($r^2 = -0.885$, $P < 0.05$). Finally, Wolf numbers were negatively correlated with the average salp abundance, spawning success, and contribution of the 3+ and 4+ age groups, while significant positive correlations were obtained with mesozooplankton biomass and the southmost position of the ice in the region of the Cooperation Sea (Table 9).

Summarizing the above findings, it seems that some similar processes, previously identified in the Atlantic sector of the Southern Ocean (Siegel and Loeb 1995; Siegel et al. 1997), may occur in the Cooperation Sea. Years with high levels of warm deepwater input to the Cooperation Sea from the north result in changes in the oceanographic structure of the region (Lanin 1993), leading to the presence of large numbers of salps north of the AD and successful krill spawning in the region. As a consequence, these years are characterized by the lowest ice coverage and subsequently followed by the intensive ice accumulation during the winter. These conditions induce high levels of recruitment of the 1+ age group in the southern part of the Cooperation Sea during the next summer season, which in turn may promote a krill biomass increase 1–2 years latter. These findings suggest that the krill life cycle is substantially affected by the prevailing oceanographic conditions in the Cooperation Sea. The prevailing oceanographic conditions also affect overall productivity and performance of the whole pelagic ecosystem (Samyshev 1991; Lanin 1993; Budnichenko 1994). However, temporal dynamics in krill biomass cannot be explained conclusively by the above mechanisms, probably due to the multiyear life cycle of Antarctic krill.

Since Antarctic krill are concentrated in the top layer of water during the summer season, the spatiotemporal dynamics of krill biomass have been suggested to be a function of atmospheric processes over the Cooperation Sea (Bryantsev et al. 1990; Samyshev 1991). Moreover, it has been suggested that atmospheric processes are probably more important and powerful than oceanographic processes (Bryantsev et al. 1990). However, it seems logical that both processes should be analyzed together, and long-term observations indicate that interannual krill biomass dynamics in the Cooperation Sea are largely dependent on annual variability in circulation patterns in both the atmosphere and the hydrosphere (Bibik and Yakovlev 1991). Since 1987, remarkable changes in atmospheric circulation activity have resulted in substantial increases in the meandering of current fields south of the AD. This has appeared to reduce the expatriation of Antarctic krill from the southern part of the Cooperation Sea northward. As a consequence, a gradual increase in krill biomass has occurred in the region south of the AD since 1988. The krill biomass peaked in 1989–1990, e.g., during years of the highest contribution of the 3+ and 4+ age groups (Bibik and Yakovlev 1991). It may therefore be postulated that the degree of the spatial separation of the southern part of the Cooperation Sea from the adjacent waters and krill life cycle dynamics are major factors underlying long-term variability in krill biomass in this region (Bryantsev et al. 1990, 1991; Bibik and Yakovlev 1991).

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Environmental constraints on the lipid composition and metabolism of euphausiids: the case of *Euphausia superba* and *Meganyctiphanes norvegica*

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Abstract: Antarctic (*Euphausia superba*) and northern krill (*Meganyctiphanes norvegica*) are characterised by large-scale spatial distributions. *Euphausia superba* is limited to the Southern Ocean, while *M. norvegica* is present from the Arctic Ocean to the Mediterranean Sea. *Euphausia superba* structural lipids showed little mesoscale variability. Specific differences between phosphatidylcholine and phosphatidylethanolamine fatty acid composition exceeded variability related to sampling stations. On a larger scale (Southern Ocean), fatty acid composition of both total polar lipids and phosphatidylcholine confirmed the reduced level of regional variability. Similar comparisons between female *M. norvegica* collected at two extreme sites in terms of temperature regime (Kattegat and Ligurian Sea) during two seasons (spring–summer and fall–winter) suggested a more complex picture. Levels of phosphatidylethanolamine, lysophosphatidylcholine, and diphosphatidylglycerol showed significant differences between sites. During spring–summer, a lower content of phosphatidylethanolamine and lysophosphatidylcholine was observed for the Ligurian Sea population. Fatty acid composition of total polar lipids was significantly different at both sites. Comparisons between spring–summer populations at both sites showed higher percentages of 22:6*n*–3 and a lower content in saturated and monoenoic acids for the Ligurian Sea, suggesting some degree of adaptation to temperature regime.

Résumé : Le krill des eaux du nord et celui de l'Antarctique (*Meganyctiphanes norvegica* et *Euphausia superba*) se caractérisent par une large distribution spatiale. *E. superba* est confinée à l'océan Austral, tandis que *M. norvegica* est présente de l'océan Arctique à la Méditerranée. Les lipides structuraux de *E. superba* présentent peu de variabilité à l'échelle moyenne. Les différences spécifiques entre la teneur en certains acides gras, la phosphatidylcholine (PC) et la phosphatidyléthanolamine (PE), dépassaient la variabilité liée aux stations d'échantillonnage. À plus grande échelle (océan Austral), la teneur en acides gras, tant des lipides polaires totaux que de la PC, confirmait la diminution de la variabilité régionale. Des comparaisons similaires entre des femelles de *M. norvegica* prélevées à deux sites extrêmes en termes de température (Kattegat et mer Ligurienne) pendant deux saisons (printemps–été; automne–hiver) ont fait ressortir une image plus complexe. Les teneurs en PE, en lysophosphatidylcholine (LPC) et en diphosphatidylglycérol (PG) présentaient des différences significatives d'un site à l'autre. Pendant la saison printemps–été, on a observé une teneur plus faible en PE et en LPC dans la population ligurienne. La composition des lipides polaires totaux était nettement différente aux deux sites. Les comparaisons entre les populations de la saison printemps–été aux deux sites a révélé de plus forts pourcentages de 22:6*n*–3 et une teneur plus faible en acides saturés et monoénoïques dans la mer Ligurienne, ce qui peut correspondre à un certain degré d'adaptation thermique.

[Traduit par la Rédaction]

Introduction

Euphausiids are widely distributed in the world ocean and have adapted to drastically different environmental conditions, both physical and biological (Mauchline 1980). Some species show a wide latitudinal distribution, while others seem to be restricted to small geographical areas (Mauchline and Fisher 1969). Most species inhabit oceanic waters, although a few live in coastal waters. Limits of distribution appear to be related to hydrographic conditions, although seasonal changes are known to occur at the boundaries of the distribution (Brinton 1962). These local changes often reflect changes in water mass distribution (temperature and current) but could also be related to food availability, predation risk, and probably physiological conditions.

At the environmental extremes, species can either be distributed within relatively homogeneous hydrographic conditions (Antarctic species) ot extend over very different hydrographic regimes from arctic to temperate and (or) subtropical conditions. Different temperature regimes are usually associated with different food webs and thus different trophic interactions between krill and food resources. The food of

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euphausiids comprises almost all particle types and planktonic organisms from phytoplankton to detritus to copepods. Some species are mostly herbivorous or mostly carnivorous, but many are omnivorous (Mauchline and Fisher 1969). Seasonality in food abundance is also variable, and each species must develop some means to cope with either periods of very low food supply (winter conditions at high latitudes) or marked seasonal changes in the nature of the food (temperate and subtropical conditions).

Studies of the combined influence of environmental temperature and trophic changes on biological processes of euphausiids are difficult because both physiological and structural adaptation should be considered. Given the dual function of lipids in living organisms, the study of neutral and polar lipids provides insights into the processes involved in adaptation. Indeed, constancy in tissue or organ function is reflected in the composition and structure of polar lipids, while neutral lipids vary widely as a result of a balance between dietary intake, anabolism, and catabolism (Sargent and Henderson 1986). Although a large body of literature has been devoted to the relationship between food assimilation and fatty acid composition of neutral lipids, far less attention has been given to the factors controlling the variability in polar lipid composition. Besides genetic differences, temperature is known to cause gel–liquid phase transformations, which result in changes in membrane fluidity (McElhaney 1984). Similarly, the fatty acid composition of food may alter synthetic pathways, mainly when ingestion of polyunsaturated fatty acids becomes limiting (Virtue et al. 1993).

In the present study, changes in polar lipids and corresponding fatty acid composition are considered in relation to temperature constraints and food supply. The central question is whether or not different thermal regimes and associated food web structure resulted in adaptive changes in structural lipids. Two euphausiid populations have been considered with respect to the drastic differences in their environment: summer Antarctic krill (*Euphausia superba*) are subject to isothermal summer conditions with high to moderate phytoplankton food supply, while northern krill (*Meganyctiphanes norvegica*) are distributed over a range of temperature conditions and display a wide range of feeding behaviours. In the context of the present paper, we will limit the data on *M. norvegica* to two extreme sites with stable deep thermal regimes, i.e., the Ligurian Sea (13°) and the Kattegat (4–6°C below the halocline), using stage 2 female krill (Cuzin-Roudy and Buchholz 1999). Evolutionary adaptation is likely, and different constraints could potentially modify lipid structure and metabolism.

Materials and methods

Sampling and sites

Euphausia superba were collected during the course of the BIOMASS cruises FIBEX (January–February 1981) and SIBEX (January–February 1985) onboard the N/O *Marion Dufresne* from RMT 8 oblique tows from 100 m to the surface. Sampling stations extended from 30 to 70°E and from 60 to 65°S. Details of the sampling stations and their position are presented in Fig. 1 for FIBEX and SIBEX. In the latter case, samples originated from stations 22C and 23. *Meganyctiphanes norvegica* were collected at night using a MOCNESS (multiple opening closing net and environmental sensing system; Wiebe et al. 1985) equipped with 2-mm-mesh nets onboard the R/V *Heincke*. Short acoustically aimed hauls were made at night in the upper layers of the water column where krill were actively feeding. Sampling sites included the Kattegat (57°16′N, 11°25′E; KATTEX cruises) and the Ligurian Sea (43°00′N, 07°00′E; LIGEX cruises) during two seasons (fall–winter and spring–summer of 1996–1998).

Lipid extraction and analysis

At all sites, individuals were sorted to stage (male and female *E. superba*, female *M. norvegica*), rinsed with distilled water, and immediately deep frozen (liquid nitrogen) and stored (–80°C). Lipid extraction and analyses were made within 3 (*M. norvegica*) to 6 months (*E. superba*) of collection. Extraction was carried out according to Bligh and Dyer (1959), and lipids were stored under nitrogen in sealed vials at –80°C. Total lipids were weighed in tared vials and concentration measured using a microbalance (±0.001 mg). Lipid classes were quantified after chromatographic separation coupled with FID detection on an Iatroscan MK III TH10 equipped with an MK IV detector (Ackman 1981). Total lipids were applied to Chromarod SIII using microcapillaries (1 µL) and analysed in duplicate (*E. superba*) or triplicate (*M. norvegica*). Details of the solvent systems used for separation of both polar and neutral lipids can be found in Mayzaud (1997) for *E. superba*. A two-stage development system was used for *M. norvegica*: neutral lipids were developed using benzene – chloroform – formic acid (60:24:1.8), while polar lipids were developed using chloroform–methanol–ammonia (50:50:5). Calibration of the rods was done using lipid classes isolated by column chromatography on silica gel (Bio-Sil HA, minus 325 mesh) followed by thin-layer chromatography on precoated silica gel plates, as suggested by Miller et al. (1998). Neutral lipids were eluted from the column with six column volumes of chloroform and polar lipids with six column volumes of methanol followed by one column volume of methanol–ammonia (5%). All operations took place under nitrogen. Separation and detection on thin-layer chromatography plates followed Mayzaud (1997).

Fatty acid methyl esters of total lipids and lipid classes were prepared either with 7% boron trifluoride in methanol (100°C, 30 min) under nitrogen (*E. superba*) or with methanol – hydrochloric acid – chloroform (10:1:1, 100°C, 1 h) under nitrogen (*M. norvegica*). *Euphausia superba* esters were analysed by gas–liquid chromatography using a 46 m length × 0.25 mm inside diameter quartz capillary column coated with Silar 5CP in a Perkin-Elmer 8320 gas chromatograph. *Meganyctiphanes norvegica* esters were analysed using a J&W 30 m length × 0.25 mm inside diameter quartz capillary column coated with SE 30 in a Perkin-Elmer XL Autolab gas chromatograph. Helium was used in all cases as a carrier gas. Individual components were identified by comparing retention time data with those obtained from authentic and laboratory standards. In addition to the examination of the esters recovered, one part of the fatty acid methyl ester samples was completely hydrogenated and the product examined quantitatively and qualitatively by gas–liquid chromatography. The results are given to one decimal place, but this does not imply this level of accuracy. Major components (>10%) should be accurate to ±5%, moderate components (1–9%) to ±10%, and minor components to up to ±30%.

Statistical treatment

Comparison of fatty acid profiles was done by multivariate correspondence analysis (Lebart et al. 1995). To facilitate the representation of the structure of the factor scores, an ascending hierarchical clustering method was used to group those observations that displayed maximum similarity to produce a number of classes represented in a dendrogram (Lebart et al. 1995). Computation was done using SPAD 3.0 software. Multiple comparisons were made

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Fig. 1. Cruise track and stations operated as part of the (*a*) SIBEX and (*b*) FIBEX cruises in the Indian sector of the Antarctic Ocean.

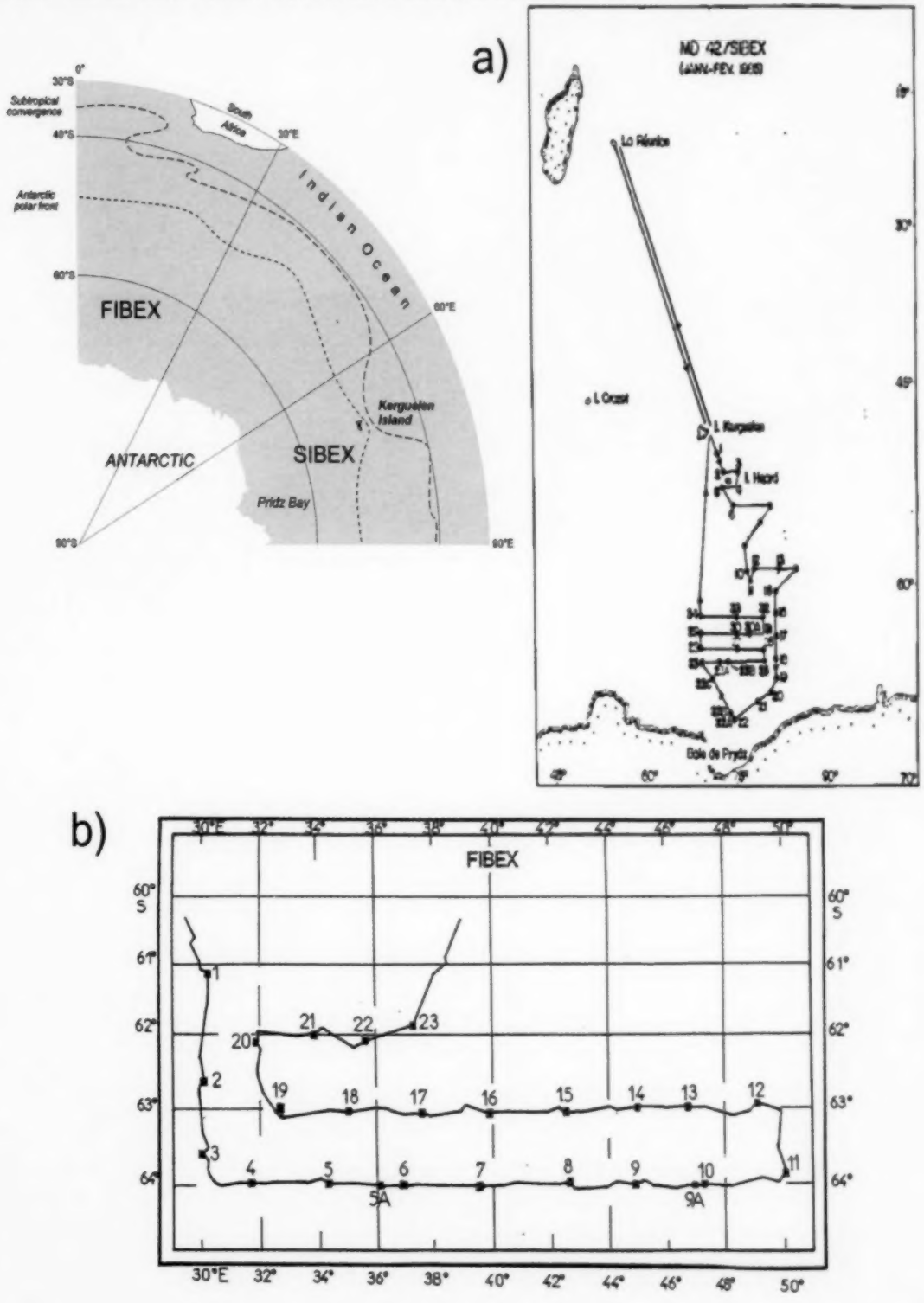

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Table 1. Composition of polar lipids (% total polar lipids) of *E. superba* in relation to sex, organ, and geographical location.

	Clarke (1980) (54–56°S, 35–39°W)				Mayzaud (1997) (60–63°S, 66–80°E)				Hagen (1988)			
									Antarctic Peninsula		Weddell Sea	
	Fem. g	Male	Ovary	Muscle	Fem. g	Male	Ovary[a]	Muscle[b]	Female	Male	Female	Male
Phosphatidylcholine	79.9	76.2	86.9	77.6	67.8	61.4	77.9	60.8	78.8	64.0	95.0	91.9
Phosphatidylethanolamine	11.9	16.2	7.5	9.2	32.2	38.6	20.3	37.9	19.9	34.0	4.4	7.5
Diphosphatidylglycerol	1.7	1.1	1.2	1.2	—	—	1.8	0.3	—	—	—	—
Phosphatidyl serine	0.7	0.8	1.2	1.2	—	—	—	—	—	—	—	—
Phosphatidyl inositol	1.2	1.5	0.2	1.9	—	—	—	—	—	—	—	—
Lysophosphatidylcholine	2.1	0.5	0.7	5.2	—	—	—	—	—	—	—	—
Lysophosphatidylethanolamine	0.7	1.6	0.2	0.1	—	—	—	—	—	—	—	—
Sphingomyelin	0.5	Trace	0.7	0.5	—	—	—	—	—	—	—	—
Phosphatidic acid	0.6	0.5	0.2	0.3	—	—	—	—	—	—	—	—

Note: Fem. g, gravid female.
[a]Cephalothorax.
[b]Abdomen.

using analysis of variance followed by Tukey post hoc tests using Systat 7.0 (Wilkinson 1996).

Results

Stable low-temperature environment: *E. superba*

Polar lipid composition

There are relatively few studies on the detailed composition of structural lipids of *E. superba*. Changes in the proportion of phosphatidylcholine (PC) and phosphatidylethanolamine (PE) with sex or organs were given by Hagen (1988), Mayzaud (1997), and Mayzaud et al. (1998), but the only full account was provided by Clarke (1980). As summarised in Table 1, PC dominated the polar lipids (60–95% polar lipids) with site-dependent concentrations (analysis of variance, $p > 0.01$). There were slightly higher values in mature females than in males and in ovary than in muscle, followed by PE (4–38% polar lipids) with complementary reverse variations with sites, sex, and organs. Other compounds made up less than 5% of polar lipids and did not show any clear pattern of changes. An atypical relationship between PC (percent wet weight) and total lipid changes has been recorded by Saether et al. (1986), Hagen (1988), Mayzaud (1997), and Mayzaud et al. (1998), which made the interpretation of the adaptive value of PC variation difficult. No such relationship was reported for PE, which showed mean values of 0.42 ± 0.08% wet weight in individuals from the Indian sector of the Antarctic Ocean (Mayzaud 1997), 0.20 ± 0.06% wet weight in those from the Antarctic Peninsula (Hagen 1988), and 0.10 ± 0.03% wet weight in those from the Weddell Sea (Hagen 1988). The possibility that the PC and PE fractions may contain significant proportions of 1-*O*-alkyl-2-acyl-sn-glycero-3-phosphocholine or -phosphoethanolamine (Sargent 1989) has not been considered but could be part of the changes recorded.

Fatty acid composition

Because polar lipids are known to reflect species characteristics rather than trophic interactions, there have been few attempts to study intraspecific variability. The fatty acid composition of PC and PE is presented in Table 2 for two areas of the Indian sector of the Antarctic Ocean. In both cases, PC was characterised by a dominance of 16:0, 20:5*n*–3 (eicosapentaenoic acid (EPA)), and 22:6*n*–3 (docosahexaenoic acid (DHA)). Intermediate constituents were 18:1*n*–9, 18:1*n*–7, 14:0, and 18:2*n*–6. PE showed basically the same features but with differences in the proportion of EPA and DHA (PC = 2 and PE = 0.7), in the ratio between 18:1*n*–7 to 18:1*n*–9 (PC = 1 and PE = 3.5), and in the lower percentages for most polyunsaturated acids with three and four double bonds.

One can anticipate that the degree of variability of polar lipids might vary with the space scale considered. Under this assumption, minimal variability is expected at the small to medium scale, while the maximum level could be anticipated for the entire Southern Ocean. At the small (FIBEX, 30–50°E) and medium scale (Indian basin, 30–75°E), the fatty acid composition of both PC and PE showed little spatial differences with longitude (Fig. 2). Indeed, clusters of stations 8–19 and 3–10 for PE or stations 11–19 and 2–23

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Table 2. Fatty acid composition (% total fatty acids) of phosphatidylcholine (PC) and phosphatidylethanolamine (PE) from *E. superba* collected during the FIBEX and SIBEX cruises in the Indian sector of the Antarctic Ocean between 62 and 64°S.

	30–50°E (N = 13)		70–75°E (N = 5)	
Fatty acid	PC	PE	PC	PE
14:0	3.53±0.55	1.23±0.44	3.44±0.56	1.02±0.36
15:0	0.44±0.17	0.37±0.37	0.26±0.04	0.21±0.10
Iso16:0	0.11±0.08	—	0.12±0.09	—
16:0	32.88±9.30	21.08±5.51	29.45±4.46	26.50±7.31
Iso17:0	0.35±0.07	—	0.30±0.11	0.45±0.16
17:0	0.20±0.13	0.32±0.30	0.26±0.01	0.22±0.08
Iso18:0	0.16±0.09	0.49±0.33	0.16±0.03	0.52±0.18
18:0	0.95±0.26	1.56±0.59	0.87±0.03	2.26±1.10
Σ saturates	38.67±8.99	25.05±6.63	34.97±4.99	31.18±9.22
16:1*n*–9	0.52±0.14	0.16±0.21	0.44±0.11	0.36±0.05
16:1*n*–7	2.25±0.49	1.16±0.24	2.38±0.42	1.51±0.32
16:1*n*–5	0.24±0.13	0.13±0.20	0.13±0.08	0.27±0.07
18:1*n*–9	5.23±1.52	4.89±1.00	6.55±1.59	7.64±1.05
18:1*n*–7	5.44±0.94	17.34±4.05	6.58±1.31	26.76±4.06
18:1*n*–5	0.12±0.11	0.30±0.28	0.14±0.03	0.47±0.07
20:1*n*–9	0.22±0.17	0.47±0.81	0.49±0.12	0.95±0.28
22:1*n*–9	0.50±0.52	0.14±0.47	1.33±0.37	—
Σ monoenes	14.52±2.77	24.17±4.58	18.03±2.70	37.97±5.34
18:2*n*–6	3.16±0.63	1.47±0.59	3.08±0.34	1.51±0.15
18:3*n*–6	0.32±0.16	0.01±0.03	0.32±0.11	—
18:3*n*–3	0.93±0.18	0.13±0.23	0.87±0.10	0.17±0.03
20:3*n*–6	0.44±0.19	0.30±0.33	0.62±0.06	0.41±0.03
Σ trienes	1.68±0.42	1.91±0.83	1.81±0.15	0.58±0.34
16:4*n*–3	0.21±0.21	0.13±0.20	0.16±0.07	0.32±0.06
18:4*n*–3	1.05±0.29	0.16±0.25	1.21±0.22	0.48±0.06
20:4*n*–6	1.25±0.54	1.52±1.17	1.37±0.25	1.29±0.39
20:4*n*–3	1.10±0.29	0.37±0.38	1.11±0.17	0.46±0.13
Σ polyenes with 4	3.61±0.77	2.17±1.34	3.85±0.55	2.54±0.28
20:5*n*–3	24.40±3.84	19.13±4.33	25.45±3.68	11.47±4.05
21:5*n*–3	0.36±0.22	—	0.78±0.31	—
22:5*n*–3	0.73±0.20	0.18±0.27	0.65±0.26	0.46±0.28
Σ polyenes with 5	25.48±3.92	19.31±4.35	26.88±4.05	11.93±4.37
22:6*n*–3	12.26±2.18	25.87±6.83	12.62±3.18	14.63±5.53
18:1*n*–7/18:1*n*–9	1.04	3.54	1.00	3.50
20:5*n*–3/22:6*n*–3	1.99	0.73	2.01	0.78
n–3/*n*–6	7.93	13.93	7.95	8.71

Note: Only fatty acids >0.1% are listed. —, not detected; N, number of stations analysed.

for PC corresponded to similar latitudes (see Fig. 1). In fact, the differences in fatty acid composition between PC and PE exceeded the spatial heterogeneity and accounted for 59% of the total variance (axis 1), while the spatial heterogeneity was essentially associated with the second axis (25% of total variance) and the PE fraction.

Larger scale variability is more difficult to understand because of the paucity of data on polar lipid fatty acid composition (Clarke 1980; Virtue et al. 1993; present data) and because data are limited to South Georgia, Prydz Bay, and the Indian sector of the Antarctic Ocean. A somewhat larger data set existed for the fatty acid composition of total lipids (Bottino 1975; Virtue et al. 1996; Phleger et al. 1998), which enlarged the geographical coverage to the Ross Sea area. To avoid mixing the influence of structural and dietary interactions, we used correspondence analysis in a slightly different way. The analysis was based on active variables (data set limited to those fatty acids reported in all studies): polar lipids and PC; supplementary variables (fatty acid profiles of total lipids) not used in the definition of the factorial axes were projected onto the planes defined by the active variables (Lebart et al. 1977). Three axes are needed to account for 93.7% of the total variance. The first one (54.7% of total variance) illustrates the fatty acid homogeneity of the structural constituents (Fig. 3*a*), as all profiles (PM70°EPol = SIBEX polar lipids excepted) of polar lipids and PC, regardless

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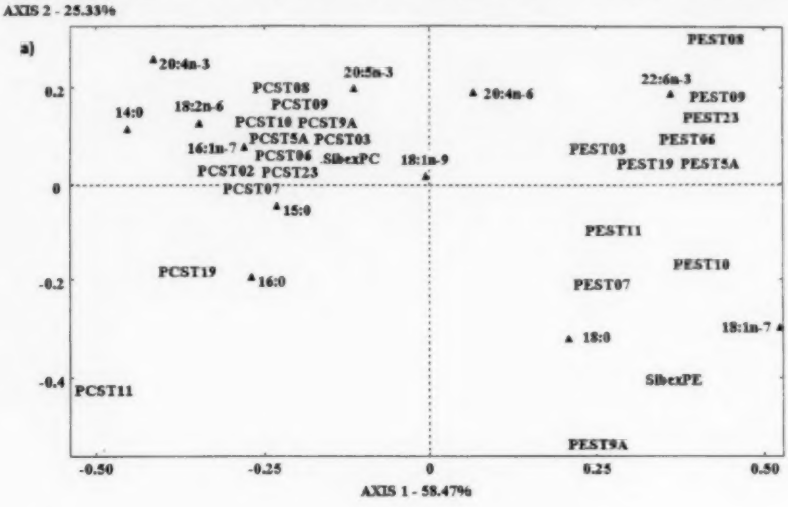
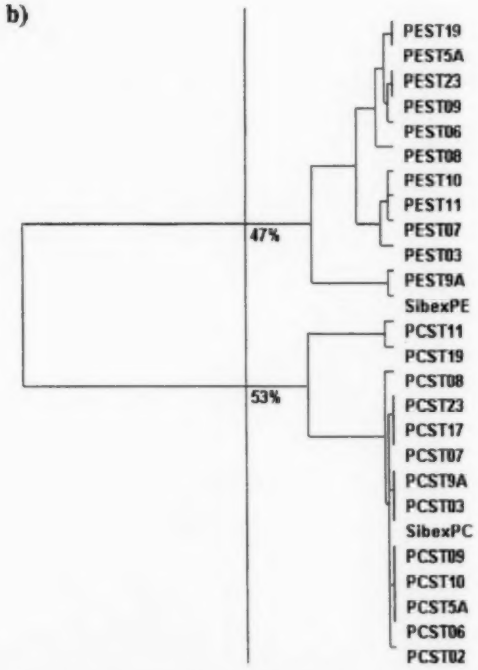
Fig. 2. (*a*) Correspondence analysis of the fatty acid composition of phosphatidylcholine (PC) and phosphatidylethanolamine (PE) from the FIBEX and SIBEX *E. superba* collections in the Indian sector of the Antarctic Ocean. (*b*) Hierarchical clustering was done on the first five principal components. Abbreviations: PEST19, for example, corresponds to the PE fatty acid profile from station 19 in Fig. 1.





of latitude and trophic conditions, showed similar coordinates on the first axis. The second axis (21.1% total inertia) separated the PC constituents form the remaining total polar lipid constituents with some geographical discrimination within each of the two lipid categories (Indian sector (30–70°E) versus South Georgia (35°W)) in relation to palmitic acid (16:0), DHA (22:6*n*–3), and oleic acid (18:1*n*–9) (Fig. 3*a*). Consideration of the supplementary variables suggested that fatty acid profiles from total lipids are discriminated along the first axis, probably in relation to the presence of triacylglycerols, which modify the fatty acid profiles. The third axis (17.8% total inertia) discriminates between *E. superba* incubated onboard ship with different food types (i.e., Phaeo, Pouch, and Mix) and field collected animals (P.M. Clarke and Phleg) based upon DHA and EPA (20:5*n*–3). It can be seen as a trophic and (or) a condition axis related to the influence of food on the polar lipid fatty acid composition (Fig. 3*b*).

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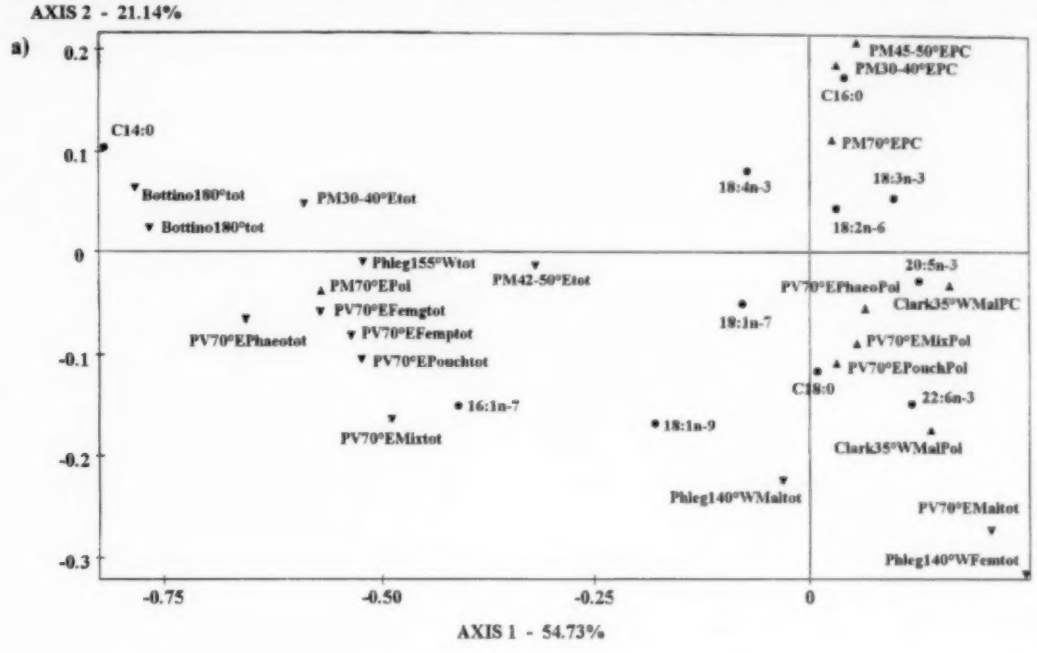
Fig. 3. Correspondence analysis of the fatty acid composition of *E. superba* total and polar lipids for all available data around the Southern Ocean. (*a*) Projection in the factorial plane defined by axes 1 and 2; (*b*) projection in the factorial plane defined by axes 2 and 3. Fatty acids from total polar lipids and phosphatidylcholine were used as active variables (triangles) and fatty acids from total lipids were used as supplementary variables (inverted triangles). Circles illustrate fatty acid descriptors. PM, present data; Bottino, Bottino (1975); Clarke, Clarke (1980); Phleg, Phleger et al. (1998); PV, Virtue et al. (1993, 1996) (numbers indicate the longitude of the sampling site); Fem, females; Mal, males; tot, total lipids; Pol, total polar lipids; PC, phosphatidylcholine; Pouch, *Phaeocystis pouchetii*; Phaeo, *Phaeodactylum tricornutum*; Mix, mixed diet. Abbreviations: PM42–50°EPC, for example, corresponds to the PC fatty acid profile from the present data at stations between 42 and 50°E; similarly, PV70°EphaeoPol corresponds to total polar lipid fatty acid profiles for krill collected at 70°E, fed a diet of *P. tricornutum*, and reported by Virtue et al. (1993, 1996).



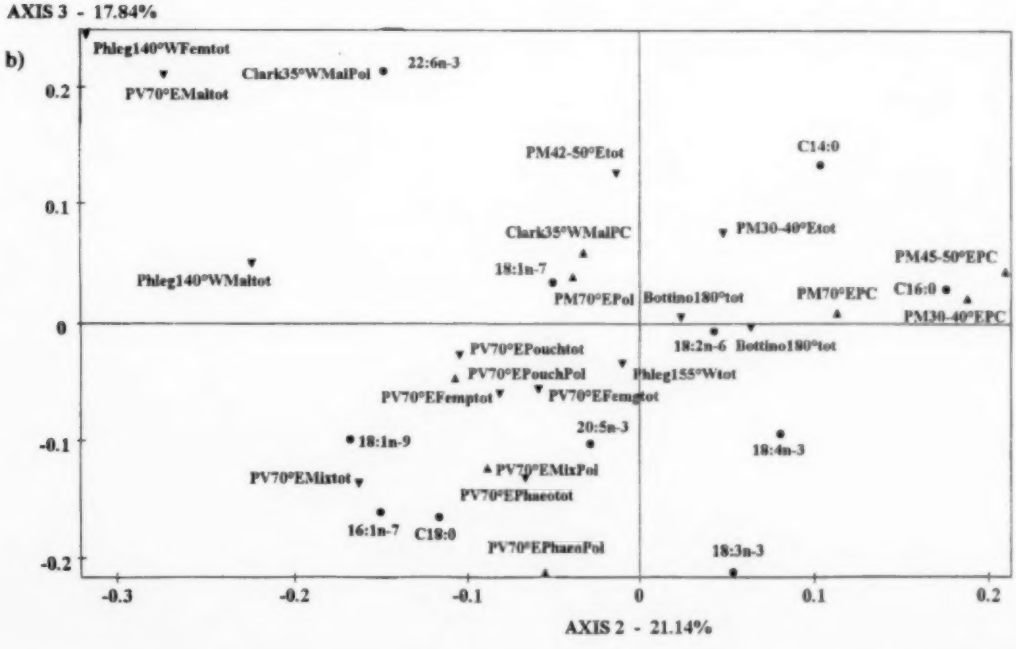


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Table 3. Lipid class composition (mg·100 mg wet weight^{-1}) of female *M. norvegica* from the Ligurian Sea (LIGEX) and the Kattegat (KATTEX) in summer–spring or fall–winter.

	LIGEX 1 (spring)	LIGEX 2 (fall)	dif	*p*	KATTEX 1 (summer)	dif	*p*	KATTEX 2 (winter)	dif	*p*
Hydrocarbons	0.04±0.02	0.07±0.04			0.19±0.12	L_1, L_2	0.002	0.04±0.02	K_1	0.001
Triacylglycerols	1.14±0.42	0.87±0.70			0.83±0.22			0.88±0.34		
Free fatty acids	Trace	Trace			0.007±0.002			0.007±0.01		
Cholesterol	0.22±0.06	0.16±0.05			0.24±0.06	L_2	0.022	0.17±0.04		
Diacylglycerols	0.09±0.04	0.11±0.05			0.17±0.06	L_1, L_2	0.018	0.09±0.02	K_1	0.001
Monoacylglycerols	Trace	Trace			0.015±0.004			0.004±0.007		
Phosphatidylglycerol	0.08±0.03	0.05±0.02	L_1	0.01	0.07±0.01			0.08±0.02	L_2	0.002
Phosphatidylethanolamine	0.22±0.03	0.37±0.12	L_1	0.05	0.37±0.18	L_1	0.05	0.24±0.04		
Phosphatidyl serine + inositol	0.14±0.03	0.17±0.05			0.19±0.11			0.11±0.03		
Phosphatidylcholine	1.66±0.30	1.09±0.34	L_1	0.02	1.50±0.3			1.31±0.21		
Lysophosphatidylcholine	0.05±0.02	0.04±0.02			0.07±0.02			0.03±0.008	L_1, L_2, K_1	0.017

Note: Trace indicates that the component occurred occasionally at concentrations <0.01 mg·100 mg wet weight^{-1}. Number of replicates = 10; dif, difference with either LIGEX 1 (L_1), LIGEX 2 (L_2) or KATTEX 1 (K_1), KATTEX 2 (K_2).

Table 4. Analysis of variance and multiple comparison test for the differences between sites during each specific season of lipid classes and ratios.

	Fall–winter (nonreproducing)			Spring–summer (reproducing)		
Factor	*F* value	df	Tukey test *p*	*F* value	df	Tukey test *p*
PE	19.28	2,26	0.0001	55.92	2,28	0.006
LPC	38.84	2,24	0.0001	—	—	ns
PG	17.25	2,26	0.004	—	—	ns
DG/PG	7.23	2,25	0.007	5.11	2,23	0.011
DG/PC	—	—	ns	4.79	2,23	0.014
LPC/PS	6.22	2,25	0.005	5.57	2,25	0.009
LPC/PG	13.03	2,25	0.0001	10.63	2,28	0.05
PE/PC	35.18	2,26	0.0001	21.16	2,27	0.001

Note: PE, phosphatidylethanolamine; LPC, lysophosphatidylcholine; PG, phosphatidylglycerol; DG, diacylglycerol; PS, phosphatidyl serine + inositol; ns, not significant.

Similar analysis considering sex and maturity stages failed to show any important contribution to the recorded spatial heterogeneity even for PE and total lipid fatty acid composition (not shown).

Variable temperature regime: *M. norvegica*

Lipid class composition

A detailed account of lipid class composition is beyond the scope of the present work. We will focus on the composition in absolute terms normalised for size differences, i.e., milligrams lipid per milligram wet weight. Size and wet weight of analysed individuals showed limited changes between the two sites, with values in the Ligurian Sea ranging from 28 to 33 mm (215–310 mg) in spring and from 31 to 34 mm (270–310 mg) in fall and values in the Kattegat ranging from 28 to 36 mm (175–330 mg) in summer and from 32 to 34 mm (206–360 mg) in winter. The results presented in Table 3 indicated that polar lipids dominated with PC and PE as major constituents. Triacylglycerol is the main neutral lipid, although free sterols and mono- and di-acylglycerols (DG) were also present. Several minor polar lipids were also recorded, e.g., phosphatidylglycerol (PG), phosphatidyl serine + inositol (PS + PI), and lysophosphatidylcholine (LPC). Summer Kattegat samples differed significantly from the Ligurian Sea ones (both seasons) in terms of hydrocarbon content (Table 3), from the Ligurian Sea spring krill in terms of PE, and from the Ligurian fall samples in terms of DG and cholesterol. Ligurian Sea samples showed significant differences among each other with regard to PG, PE, and PC. Kattegat winter samples differed from those of summer in terms of hydrocarbons, DG, and LPC and from the Ligurian samples (both seasons) in terms of PG (Table 3).

To appreciate the influence of mean environmental temperature, we selected those lipid constituents (or ratios) that showed significant differences with mean thermal regime (i.e., site) in each season sampled. A common set of descriptors displayed a relationship with temperature for both seasons: PE, DG/PG, LPC/PS + PI, LPC/PG, and PE/PC (Table 4). Additional descriptors were also significantly associated with sites but at a single season: LPC, PG, PG/PE, PS/PC, LPC/PC, and PG/PS (fall–winter nonreproducing season) and DG/PC (spring–summer reproducing season). Opposite patterns of change were observed for each season (Fig. 4), with higher concentrations or ratios at 13°C (Ligurian Sea) than at 4°C during the nonreproducing season and the reverse for the an-

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Fig. 4. Changes in *M. norvegica* polar lipid concentration and ratios among polar lipid constituents for the Ligurian Sea (13°C) and the Kattegat (4°C) in (*a*) fall–winter (nonreproducing season) and (*b*) spring–summer (reproducing season). Only significant differences ($p < 0.05$) are shown. PE, phosphatidylethanolamine; LPC, lysophosphatidylcholine; PG, phosphatidylglycerol; DG, diacylglycerol; PS, phosphatidyl serine + inositol; PC, phosphatidylcholine. Solid bars, 4°C environmental temperature; open bars, 13°C environmental temperature.

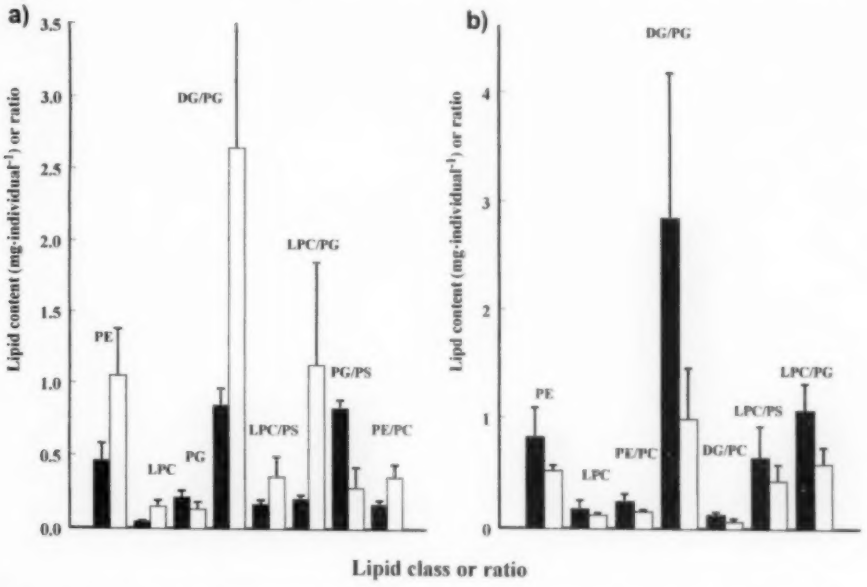

Table 5. Potential effect of environmental temperature on fatty acid composition of phospholipids of *M. norvegica* collected in the Kattegat (KATTEX) and the Ligurian Sea (LIGEX) (number of individuals analysed = 3).

	Weight (%)					
Fatty acid	KATTEX 1 (4°C)	LIGEX 2 (13°C)	Δ 13°C – 4°C	KATTEX 2 (4°C)	LIGEX 2 (13°C)	Δ 13°C – 4°C
14:0	1.2	1.7	0.5	1.3	1.0	–0.3
16:0	18.0	16.6	–1.4	20.4	18.0	–2.4
18:0	1.4	2.8	1.4	1.5	2.2	0.7
20:0	0.0	0.7	0.7	0.0	0.1	0.1
Σ saturates			1.2			–1.9
16:1*n*–7	1.6	0.7	–0.9	0.3	0.6	0.3
18:1*n*–9	9.0	11.0	2.0	9.9	14.3	4.4
18:1*n*–7	3.6	3.0	–0.6	4.9	2.8	–2.1
20:1*n*–9	0.4	0.0	–0.4	1.0	0.7	–0.3
Σ monoenes			0.1			2.3
18:2*n*–6	2.0	2.5	0.5	1.0	2.8	1.8
18:3*n*–3	0.5	1.6	1.1	0.1	0.9	0.8
18:4*n*–3	0.2	1.0	0.8	0.3	0.3	0.0
20:5*n*–3	20.0	15.9	–4.1	24.0	16.5	–7.5
22:6*n*–3	37.1	36.3	–0.8	29.5	34.8	5.3
Σ polyenes			–2.5			0.4

Note: Fatty acids listed are restricted to those showing significant variations with temperature in one season (for complete composition, see Virtue et al. 2000).

imals collected during the reproducing season. As will be discussed later, if heterogeneity of structural lipids is related to local conditions or sites, the environmental or biological factors involved are complex.

Fatty acid composition

The polar lipids of *M. norvegica*, like most zooplankton, are characterised by high levels of polyunsaturated fatty acids, mainly EPA and DHA (Table 5). Detailed fatty acid

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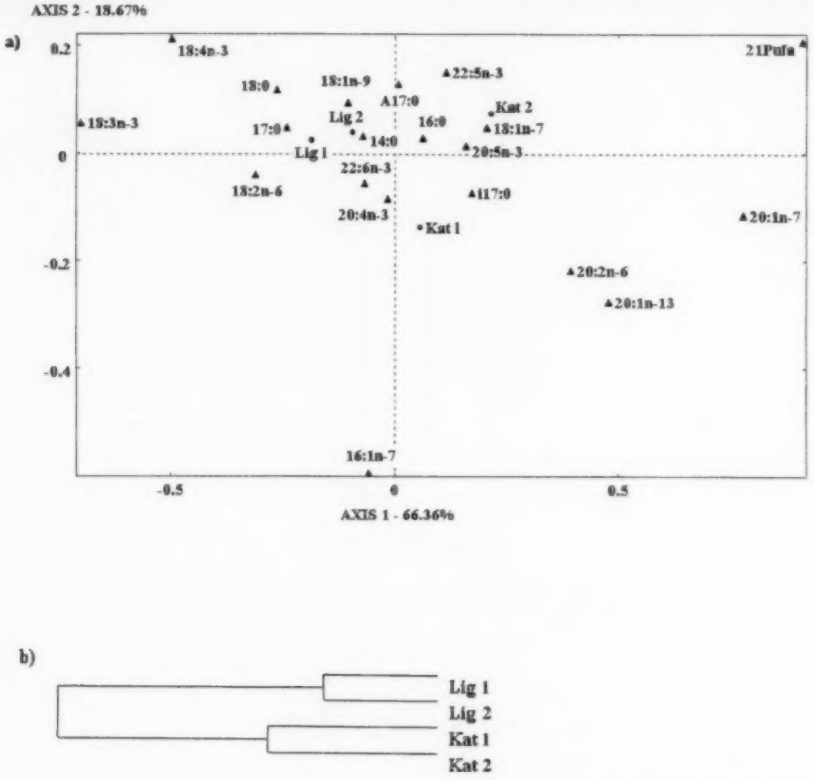
Fig. 5. Correspondence analysis of the fatty acid composition of *M. norvegica* polar lipids in two seasons in the Ligurian Sea (Lig) and the Kattegat (Kat). Hierarchical clustering is based on the first three factorial axes. Pufa, polyunsaturated fatty acids.



composition of both neutral and polar lipids at the different sampling sites is provided in Virtue et al. (2000), and the present account will be limited to the differences between the two study sites and the data directly relevant to temperature adaptation. The comparison of the total polar lipid composition between the Kattegat and the Ligurian Sea was done using multivariate correspondence analysis followed by hierarchical clustering. The results presented in Fig. 5 clearly discriminated the Ligurian population from the Kattegat one, irrespective of season. The first two axes explained 85% of the total variance, and projection of fatty acids (Fig. 5) indicated that if the first axis is related to site differences with C18 polyunsaturated acid and DHA as Ligurian descriptors and C20 fatty acid and *n*–7 acids as Kattegat descriptors, the second axis separated the winter and summer population from the Kattegat in relation to the changes in 16:1*n*–7.

Changes in unsaturation with sites or environmental temperature have been considered on a subset of the polar lipid fatty acid data (Table 5). Some changes were common to both seasons: an increase in EPA, 16:0, and 18:1*n*–7 and a decrease in 18:1*n*–9, 18:2*n*–6, 18:3*n*–3, 18:0, and 20:0. During the nonreproducing season (fall–winter), we noticed a decrease in DHA with no equivalent during the reproductive season. The total picture is relatively complex, with a decrease in saturated and monoenoic acids and an increase in polyunsaturated acids during spring–summer and an increase in saturates and a decrease in monoenoic and polyunsaturated acids during fall–winter period.

Discussion

Factors that have been found to influence polar lipid structure and fatty acid composition include species (Love 1988), genetic strains (Erickson 1992; Hoffman and Prinsloo 1995), temperature (Farkas 1979; Suutari et al. 1996), and physiological and nutritional status (Chu and Ozkizilcik 1995; Soudant et al. 1997). Ideally, each of these factors should be studied independently in controlled systems, but the techniques for rearing zooplankton are suitable for very few species. Hence, in order to study the aspects of lipid metabolism, krill species in which most of the environmental and biological variables are understood should be used. The choice of euphausiids in this study seemed appropriate, since both *E. superba* and *M. norvegica* have been the subject of extensive work (see review by Mauchline and Fisher 1969) and showed opposite patterns of distribution with respect to environmental gradients. *Euphausia superba* is limited to but widespread around the Antarctic Ocean and survives in an isothermal hydroregime associated with high seasonality in food supply (Conover and Huntley 1991). *Meganyctiphanes norvegica* is present from the Arctic Ocean to the Mediterra-

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nean Sea and the Azores and has adapted to very different physical as well as trophic conditions.

With natural populations, it is important to assess the relative influence of the various factors responsible for the polar lipid changes. Genetic influence (faster growing strains) is probably limited in *E. superba*, as no genetic differentiation has been found in any of the subpopulations sampled (Fevolden and Scheppenheim 1989). It should be also limited for *M. norvegica*, since Ligurian and Kattegat populations display similar growth rates (J.P. Labat, Observatoire Océanologique, Villefranche sur mer, France, personal communication). Physiological differences are often linked to seasonality, growth, sex, or maturation stage (Clarke 1980), and these factors can be minimised when comparisons are limited to animals of similar growth rates, sex, and maturity stages at a given period of the year. Temperature is known to cause gel–liquid phase transformations that result in changes in membrane fluidity. Organisms have evolved adaptive responses to maintain appropriate membrane liquidity (McElhaney 1984): changes in the degree of fatty acid unsaturation, variation in chain length, branching, and cyclisation of fatty acids, and changes in the distribution and proportion of glycolipids, phopholipids, and other lipid families have been shown (Neidleman 1987). Increased acyl chain unsaturation in cell membrane phospholipids is one mechanism often cited as an adaptation to cold temperature, but several results are contradictory and reverse patterns have been reported (Vaskovsky 1989). Feeding on high polyunsaturated fatty acid or low polyunsaturated fatty acid lipid sources or fasting can modify the composition of structural lipids as well as alter the relationship between *n*–3 and *n*–6 fatty acids (Hoffman and Prinsloo 1995).

In the present study, *E. superba* summer populations feed mostly on phytoplankton and undergo little changes in temperature regime. As a result, one could expect minimum changes in structural lipids within the different subpopulations and a pattern of polar lipids possibly reflecting evolutionary adaptation to extremely cold waters. The results partially confirmed this hypothesis, with medium- and large-scale spatial changes that failed to show major east–west variability but instead reflected the structural differences between polar lipid families and a north–south heterogeneity that appears to be linked to trophic interactions (Mayzaud et al. 1998). Diversity in sex and maturity stage had little influence on the overall polar lipid structure variability, but this conclusion needs further confirmation owing to the very limited data set available. This relative structural homeostasis was not associated with obvious structural adaptation to low temperature. Indeed, polar lipid composition was relatively similar for both *E. superba* and the northern more temperate species *M. norvegica*. A direct comparison of the proportion of lipid families is made difficult by the relationship between PC and total lipids in *E. superba* but is possible for PE (as percent wet weight), which indicated similar content (0.1–0.4% for *E. superba* and 0.2–0.4% for *M. norvegica*). Levels of unsaturation of polar lipids were different but showed no coherence with any scheme of temperature adaptation. As suggested by Clarke (1988), the intuitive assumption that life at 0°C must be severely constrained by temperature may not be as simple as it seems. Indeed, fatty acids of polar lipids are highly unsaturated in all marine animals (Ackman 1967; Ackman et al. 1970), and compensation may not be needed to cope with life at high latitudes. How animals cope with high rather than low temperature may be the actual question at issue here. The differences between the two euphausiids are likely species specific and related to the difference in trophic interactions: herbivorous species showed 20:5*n*–3 > 22:6*n*–3, while omnivorous or carnivorous species showed the reverse (Ackman et al. 1970).

Unlike the polar *E. superba*, the northern krill *M. norvegica* seemed to show an indication of adaptive changes to local conditions. Liguran Sea and Kattegat populations show genetic divergence in response to the isolation of the Mediterranean communities (Zane et al. 2000), and long-term acclimation to specific thermal and trophic regimes may have taken place. Differences in content of PE and LPC and various ratios among polar lipid classes were observed between the Ligurian Sea and Kattegat populations but with inverse relative proportions during the spring–summer reproducing season and the fall–winter sexual rest. Because of the generally high content of 20:5*n*–3 and 22:6*n*–3 and the lower level of shorter chain saturated and monoenoic acids of PE (Bottino 1975; Clarke 1980; this study), an increase in the relative proportion of these constituents, without significant changes in PC, should raise the degree of unsaturation of the polar lipids. As shown by Brichon et al. (1980), PE and PC compositions are strongly affected by environmental temperature, while other polar lipids (PS and PI) remain unaffected. Brichon et al. (1980) and Hazel (1985) showed that polar lipids from crabs and trout gill acclimated at increasing temperatures displayed a decrease in PE with increasing temperature. If the same model applies to longer term adaptation and *M. norvegica*, then the pattern observed in spring–summer would illustrate adaptation to environmental temperature, with increases in PE and LPC at 4°C associated with an increase in the percentages of 20:5 and, to a minor extent, 22:6. Changes in LPC as well as proportions between DG, LPC, and other polar lipids such as PG, PS, and PC could be related to the degree of synthesis of membrane lipid during long-term adaptation to the mean temperature regime.

If the pattern observed previously is actually indicative of temperature adaptation, the reverse pattern recorded during the fall–winter season strongly suggested that other factors are influential. Two sets of factors could explain the difference: (*i*) the lipid structure recorded is based on whole animals, and at times, the occurrence of specific characteristics of given organs (e.g., digestive gland or ovary) may alter the temperature adaptation signals (preliminary data on the muscle tissue of the abdomen suggest that the reversal is mostly associated with the cephalothorax fraction) and (*ii*) differential responses to poor feeding conditions could result in changes in phospholipids and modify the fatty acid composition. Indeed, in fall, *M. norvegica* in the Ligurian Sea faced low food conditions and their gut contents (P. Mayzaud, unpublished data) suggest that they rely on copepods (mostly *Centropages typicus* and *Euchirella rostrata*) as well as all particles present (radiolarians, dinoflagellates, amorphous material, etc.). During the winter in the Kattegat, the animals appear to feed to a greater extent on phytoplankton than in the Ligurian Sea (fall period) and also to feed on copepods (*Calanus* spp.)

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(P. Mayzaud, unpublished data). Virtue et al. (1997) showed that during starvation, the polar lipids of *E. superba* could be partly catabolised to meet metabolic requirements, with changes in the proportion of 20:5 indicative of differential PC utilisation. Similarly, Virtue et al. (1993) showed that different food sources affected the fatty acid composition of phospholipids in relation to the abundance of 20:5 in the dietary phytoplankton assimilated. At the present time, the pathways relating feeding conditions and structural lipid changes remain purely hypothetical. Both hypotheses will require further testing to clarify the pathways and interactions involved.

In conclusion, the majority of studies showing clear responses of lipid structure and metabolism to temperature have used differences of at least 15–20°C. Below this range of temperature differences, the response was not clearly evident, suggesting that on an evolutionary scale, marine animals need little degree of adaptive capability. Polar species like *E. superba* do not need to adapt because seasonality in food supply is probably a more important constraint than temperature (Clarke 1988). On the contrary, temperate species that colonised very different environments with variable seasonality in temperature regime and in food supply apparently undertook adaptive processes to compensate for these constraints. The present results suggest that zooplankton may face more severe selection when living in warmer water with little seasonality and oligotrophic conditions.

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Use of fatty acids as dietary indicators in northern krill, *Meganyctiphanes norvegica*, from northeastern Atlantic, Kattegat, and Mediterranean waters

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Abstract: Fatty acids of the triacylglycerol (TG) and polar lipid (PL) fractions were compared from northern krill, *Meganyctiphanes norvegica*, sampled in the Clyde Sea in the Atlantic, the Kattegat at the Alkor Deep, and the Ligurian Sea in the Mediterranean. Possible biotransformations of fatty acids in the food chain were examined in mixed zooplankton and krill faecal material from the Ligurian Sea and Kattegat. The Ligurian Sea population was distinguished from the Kattegat and Clyde Sea populations in terms of both TG and PL fatty acid profiles. The Kattegat and Clyde Sea populations were separated from each other in terms of their PL fatty acid profiles only. Krill sampled in winter from all sites had significantly higher levels of 20:1 and 22:1 fatty acids in the TG fraction (9–17%) than krill sampled in summer (1–10%). These fatty acids in particular indicate carnivorous dietary input, as they are found in high levels in copepods, which are the major prey species of *M. norvegica*. Levels of 22:6(*n*–3) were significantly higher than 20:5(*n*–3) in Ligurian krill, which, together with other specific marker fatty acids, suggested a predominance of dinoflagellates and other nondiatom species in their diet. TG fatty acids in Kattegat and Clyde Sea krill indicate a predominance of diatoms in the diet.

Résumé : Nous avons comparé les fractions trialcylglycérol (TG) et lipides polaires (LP) des acides gras chez des spécimens de *Meganyctiphanes norvegica* prélevés en mer de Clyde, dans l'Atlantique, au Kattegat dans la fosse Alkor, et dans la mer Ligurienne en Méditerranée. Nous avons examiné les biotransformations possibles des acides gras dans la chaîne trophique en étudiant du zooplancton mélangé et de la matière fécale de krill de la mer Ligurienne et du Kattegat. La population ligurienne se distinguait de celles du Kattegat et de la mer de Clyde par les profils des acides gras, tant TG que LP. Les populations du Kattegat et de la mer de Clyde se distinguaient l'une de l'autre seulement par leurs profils des acides gras TG. Le krill capturé en hiver à toutes les stations présentait des niveaux significativement supérieurs des acides gras 20:1 et 22:1 dans la fraction TG (9–17%) que le krill échantillonné en été (1–10%). Ces acides gras en particulier indiquent des apports d'alimentation carnivore, car on les retrouve en fortes concentrations chez les copépodes qui sont la proie principale de *M. norvegica*. Les niveaux de 22:6(*n*–3) étaient nettement plus élevés que ceux de 20:5(*n*–3) chez le krill ligurien, ce qui, en combinaison avec d'autres acides gras qui sont des marqueurs spécifiques, indique une prédominance des dinoflagellés et d'autres espèces autres que des diatomées dans leur alimentation. La présence d'acides gras TG chez le krill du Kattegat et de la mer de Clyde indique la prédominance des diatomées dans l'alimentation de ces crustacés.

[Traduit par la Rédaction]

Introduction

Northern krill, *Meganyctiphanes norvegica*, are an integral component of the pelagic community in the northern hemisphere and are a major food source for many carnivorous species including fish, birds, and whales (Pearcy et al. 1979). This species of krill occupies diverse habitats from the Arctic to the Mediterranean and from western Europe to the east coast of Canada. *Meganyctiphanes norvegica* undergoes diurnal vertical migrations of typically 500 m, although this migration can be in excess of 1 km (Mauchline 1980). Unlike other euphausiids, *M. norvegica* survives within a wide

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Table 1. Sampling dates, position, and season and reproductive status of cruises conducted in this study of *M. norvegica*.

	Clyde Sea		Laso Deep, Kattegat		Ligurian Sea in the Mediterranean	
	Scotex I	Scotex II	Kattex I	Kattex II	Ligex I	Ligex II
Date	22 June – 11 July 1996	20 Feb. – 4 Mar. 1997	14–29 July 1996	7–19 Mar. 1997	6–27 Apr. 1996	5–24 Sept. 1997
Position	55°48′N, 5°12′W	55°48′N, 5°12′W	57°16′N, 11°25′W	57°17′N, 11°25′W	43°16′N, 7°25′E	43°16′N, 7°25′E
Season	Summer, reproductive	Winter, nonreproductive	Summer, reproductive	Winter, nonreproductive	Winter, reproductive	Summer, nonreproductive

temperature range of 2–15°C. These diverse habitats and the high biomass of krill reflect their ability to physiologically adapt to different environments.

Various studies on individual populations of *M. norvegica* have been conducted (Matthews 1973; Buchholz and Prado-Fiedler 1987; Labat and Cuzin-Roudy 1996). To date, however, comparative investigations of these populations in relation to environmental parameters have not been conducted. How this one species has adapted to such contrasting environments is not well understood.

In this study, *M. norvegica* samples were collected from the northeastern Atlantic, Kattegat, and Ligurian Sea (from the Scotex, Kattex, and Ligex expeditions, respectively). The hydrographical conditions (temperature, salinity, and depth) at these sites vary substantially. In the northeastern Atlantic off western Scotland (the Clyde Sea), the water is relatively shallow (160 m) and cool (6–13°C) and conditions are stable. The Danish Kattegat is a highly stratified shallow water body (150 m) where temperatures vary between 2 and 18°C, while the Ligurian Sea is characterised by deep water (2000 m) that is warm (13–22°C) and stable throughout the year.

Meganyctiphanes norvegica is primarily a carnivorous species; however, it also feeds on phytoplankton. Recent studies have used stomach analyses from both field and laboratory studies to evaluate the degree of carnivory in *M. norvegica* (Bamstedt and Karlson 1998; Lass et al. 2000). Lipid analysis is a complementary method of evaluating dietary input, although like most methods has its strengths and limitations.

Lipid content and fatty acid composition of *M. norvegica* have been previously reported (Sæther et al. 1986). In fact, there is substantial literature on lipids in euphausiids because of commercial interest and their undisputed importance in marine ecosystems (Virtue et al. 1996; Mayzaud et al. 1998). Lipid compounds can be useful biochemical probes, and the information gained from fatty acid analysis can be used to understand and identify food web interactions (Mayzaud et al. 1976; Virtue et al. 1993*a*, 1993*b*).

To further understand food web interactions and seasonal variability in physiological condition, fatty acids of *M. norvegica* were analysed from three different habits: the Atlantic, the Kattegat, and the Ligurian Sea. The feeding ecology of these three populations of krill was examined to determine the influence of environment on both the triacylglycerol (TG) and polar lipid (PL) fatty acid profiles. Mixed zooplankton samples and krill faecal material were analysed to address the process of biotransformation of fatty acids through the food chain.

Methods

Sampling and site description

All krill were collected by a MOCNESS (multiple opening closing net and environmental sensing system) with 330-μm- and 2-mm-mesh nets aboard the R/V *Heincke*. Short acoustically aimed hauls of krill were made at night in the upper layers of the water column where the krill were actively feeding. Krill were frozen immediately in liquid nitrogen and maintained at –80°C until analysis. Sampling sites and cruise dates are indicated in Table 1. Faecal material was collected from krill maintained live onboard for up to 12 h after capture. Faecal material was thoroughly cleaned manually (using tweezers under a dissecting microscope) to remove all

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other particles. Faecal samples were pooled to achieve a wet weight of 0.01 g so as to decrease analytical error; hence, only one sample was available for both Ligurian Sea and Kattegat krill. Mixed zooplankton samples were taken at night at various depths using the MOCNESS equipped with 330-μm-mesh nets. The Ligurian sample was composed of several species including *Euchirella rostrata*, *Calanus helgolandicus*, *Centropges typicus*, *Oithona* sp., and crustacean nauplii. The species composition of the Kattegat samples included *C. helgolandicus*, *Calanus finmarchicus*, *Paracalanus parvus*, *Pseudocalanus* sp., and *Temora longicornis*.

Lipid extraction and analysis

All samples were quantitatively extracted using the modified Bligh and Dyer (1959) method consisting of a one-phase solvent mixture of methanol–chloroform–water (2:1:0.8, v/v/v). Samples were extracted overnight and the phases were separated the following day by addition of chloroform and water (final methanol–chloroform–water solvent ratio 1:1:0.9, v/v/v). The total solvent extract was concentrated (solvents removed in vacuum) using rotary evaporation at 30°C. All samples were made up to a known volume in chloroform and stored at –80°C. Each sample consisted of three whole krill, which were batched (either male or female). Triplicate samples were analysed (i.e., $N = 3$ (3) (three samples each consisting of three krill)) except where indicated. Krill fresh weight ranged from 0.3 to 0.5 g.

Total lipid content was determined gravimetrically. Neutral lipids (after separation of the hydrocarbon fraction) and PL were separated by column chromatography on silica gel (Bio-Sil HA, minus 325 mesh). These fractions were eluted with six volumes of hexane, chloroform, and methanol, respectively. Purity of fractions was confirmed by chromatographic separation coupled with flame ionization detection on an Iatroscan Mark III TH 10 flame ionization detector (Ackman 1981).

Lipid classes were treated with methanol – hydrochloric acid – chloroform under nitrogen (10:1:1, v/v/v, 100°C, 1 h) to form fatty acid methyl esters. Following the addition of water, products were extracted into hexane–chloroform (4:1, v/v, three times 1.5 mL), transferred to vials, reduced under a stream of nitrogen, and stored in chloroform. Alcohols were obtained via saponification of a portion of the total lipid fraction by reaction at 80°C for 3 h using 3 mL of 5% KOH in 80% methanol (w/v). Following the addition of water, products were extracted into hexane–chloroform (4:1, v/v, times times 1.5 mL), transferred to vials, and reduced under a stream of nitrogen. Gas chromatographic (GC) analyses were performed with a Perkin Elmer XL GC equipped with a J and W fused silica capillary column (SE-30), a flame ionization detector, and a split injector system. Helium was used as the carrier gas. Individual components were identified by comparing retention time data with those obtained for authentic and laboratory standards and using gas chromatographic – mass spectrometric (GC-MS) data. GC results are subject to an error of ±5%. For ease of reporting, only a limited data set is tabulated, specifically those addressed in the text and other major fatty acids. All data under 0.5% and others not referred to in the results and discussion and not reported. The full data set is available from the author. GC-MS analyses of selected samples were performed on a Fisons MD 800 GC-MS (Manchester, U.K.) fitted with an on-column injector. The GC-MS was operated in scan mode with an ionising voltage of 70 eV. The GC was fitted with a capillary column similar to that described above.

Statistical analysis

Analysis of variance (ANOVA) was conducted with the StatviewII package followed by a Fisher's PLSD (protected least significant difference) multiple comparison test. ANOVAs were performed on each fatty acid. A Bonferroni correction test was performed, and only when $P < 0.001$ did we declare variance to be significant. Mean results are reported in the text. Correspondence analysis (Benzecri 1969; Gower 1987) was performed on a data matrix transformed to relative frequencies and scaled so that each row (or column) can be viewed as a row (or column) of conditional probability distribution. Distances between profiles were computed with χ^2 metrics. This distance gives symmetry to the two sets of data so that each factorial axis of the cloud of variables corresponds to a factorial axis of the cloud of observations. Thus, it was possible to simultaneously represent descriptors and observations on the plane defined by the factorial axes. To facilitate the representation of the structure of the factor scores, an ascending hierarchical clustering method was used (Lebart et al. 1995) to group those observations that displayed maximum similitude and to produce a number of classes best represented in a dendrogram. Computation of multivariate tests was made using SPAD 3.0 software (Lebart et al. 1995). Both PL and TG fatty acids from whole male and female krill were analysed.

Results

Although results were not significant, higher lipid levels were found in krill from the Clyde Sea (4% wet weight) compared with krill from the Kattegat and Ligurian Sea (2–3%). *Meganyctiphanes norvegica* is characterised by high levels of ω-3 polyunsaturated fatty acids (PUFA), particularly in the PL fractions (47–62% of the total PL fatty acids). PUFA levels of the TG fractions were significantly lower in female krill (20–35%) compared with male krill (30–40%) in the reproductive seasons (Scotex I, Kattex I, and Ligex I) (Table 2). Conversely, PUFA levels of the PL fraction were significantly higher in female krill (58–62%) compared with male krill (47–53%) in the reproductive seasons (Table 3). There were no significant differences between male and female krill PUFA levels during the nonreproductive seasons (Scotex II, Kattex II, and Ligex II).

Krill sampled in winter from all sites had significantly higher total levels of 20:1 and 22:1 fatty acids (including 20:1(*n*–9), 20:1(*n*–7), 22:1(*n*–11), and 22:1(*n*–9)) (9–17%) in the TG fraction than krill sampled in summer (1–10%). Some minor fatty acids fluctuated with site. Fatty acid 18:4(*n*–3) was found in all samples, with Ligurian samples having 2–4%, Clyde samples having 1–3%, and Kattegat samples having 1–2%; 16:1(*n*–13)*t* was detected in Ligurian and Kattegat samples (1%) and 18:5(*n*–3) was found only in Ligurian samples (1–2%). Others ((16:4(*n*–3) and 16:1(*n*–7)) fluctuated with both season and site (Table 2).

There were no significant differences in the fatty acid and fatty alcohol profiles of zooplankton caught in the Kattegat between the two depth ranges (Tables 4 and 5). Lipid levels, however, differed significantly, with higher levels found in animals from surface waters (Table 4). There were also major differences between the Kattegat- and the Ligurian-caught zooplankton, particularly in levels of 18:4(*n*–3), 18:1(*n*–9), and the long-chain monounsaturated fatty acids. Total lipid content in faecal samples from animals from both locations was 1% wet weight. Faecal fatty acids were lower in PUFA and higher in saturated fatty acids than zooplankton and krill fatty acids. Faecal material had high levels of 18:2(*n*–6) (16–20%) and 18:0 (14–22%) compared with all other samples (1–3 and 1–7%, respectively). Major differences were found between the fatty alcohol profiles of the Ligurian and Kattegat zooplankton samples. The sum of saturated fatty alcohols in Ligurian zooplankton was 89% compared with 17–22% in

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Table 2. Percent lipid composition and total lipid (mean (±SD)) of selected TG fatty acids in whole *M. norvegica* from the Kattegat and the Clyde and Ligurian seas (N = 3 (3) (three samples each consisting of three krill)).

	Scotex I		Scotex II		Kattex I		Kattex II		Ligex I		Ligex II	
Fatty acid	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Sum saturated	27.2	30.5	22.3	24.8	31.2	30.5	27.9	27.8	34.4	40.3	33.5	31.3
Sum branched	1.3	1.5	1.1	1.1	1.6	2.2	1.6	1.6	1.5	0.5	1.6	0.8
16:1(*n*–7)	8.7	8.9	3.3	2.4	13.2	9.3	10.2	10.5	2.6	2.1	2.4	3.1
16:1(*n*–13)*t*	0.3	0.4	0.8	0.2	1.0	1.4	0.5	0.4	0.7	2.1	0.6	0.7
18:1(*n*–9)	10.6	13.7	10.6	13.5	10.9	17.4	9.6	12.9	10.7	13.0	12.2	12.3
18:1(*n*–7)	7.4	9.2	5.4	5.5	4.6	9.1	7.3	7.9	5.5	5.1	3.8	4.8
20:1(*n*–13)	0.2	0.5	0.4	0.3	0.4	0.7	0.3	0.2	0.4	0.4	0.2	0.2
20:1(*n*–11)	0.2	0.5	0.5	0.2	0.4	0.4	0.4	0.5	0.1	0.2	0.3	0.5
20:1(*n*–9)	4.7	5.6	12.1	8.5	1.4	2.2	8.6	8.6	1.7	0.6	3.5	5.3
20:1(*n*–7)	0.9	1.2	0.6	1.2	0.9	1.4	0.9	1.0	0.4	0.1	0.4	0.8
22:1(*n*–11)	2.5	0.6	2.6	3.2	1.3	1.7	5.3	3.7	0.5	0.0	0.8	0.9
22:1(*n*–9)	0.8	1.1	0.5	1.0	0.4	0.4	0.7	0.8	0.3	0.0	0.5	1.0
Sum monounsaturated	37.6	43.5	37.9	37.1	36.8	47.1	45.5	48.3	23.9	23.9	25.9	31.0
16:4(*n*–3)	2.5	2.1	1.0	0.4	0.4	0.4	4.5	1.7	0.2	0.0	0.2	0.1
18:5(*n*–3)	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.6	1.6	1.7
18:4(*n*–3)	3.4	2.6	2.7	1.3	1.4	1.1	2.3	1.0	4.0	4.2	2.2	1.5
18:2(*n*–6)	1.3	1.3	2.1	1.5	2.5	2.8	1.2	0.1	2.1	2.2	2.5	2.1
18:3(*n*–3)	0.5	0.6	1.2	0.6	0.7	1.0	0.4	0.1	2.1	1.8	1.2	0.7
20:5(*n*–3) EPA	13.1	9.5	15.0	20.7	13.7	6.5	7.8	9.9	9.0	5.3	7.8	9.2
22:6(*n*–3) DHA	10.6	6.4	13.7	10.8	10.3	6.4	6.6	8.2	21.1	16.9	21.3	19.1
22:5(*n*–3)	0.7	0.5	0.8	0.5	0.3	0.4	0.7	0.4	0.0	0.9	0.7	0.8
Sum polyunsaturated	33.9	24.5	38.6	37.0	30.5	20.1	25.1	22.3	40.2	35.3	39.0	36.9
Total 20:1 + 22:1	9.5	9.8	16.8	14.6	5.0	7.1	16.5	15.1	3.5	1.3	5.8	8.8
Total lipid (% wet weight)	4.0 (1.2)	4.1 (0.5)	3.9 (0.7)	3.7 (0.5)	2.3 (0.4)	2.1 (0.6)	3.0 (0.6)	2.9 (0.6)	3.4 (0.7)	3.1 (1.0)	2.5 (1.0)	2.4 (0.9)

Note: Mean fatty acid values and only fatty acids mentioned in text are presented for clarity.

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Table 3. Percent composition of selected PL fatty acids in whole *M. norvegica* from the Kattegat and the Clyde and Ligurian seas (N = 3 (3) (three samples each consisting of three krill)).

	Scotex I		Scotex II		Kattex I		Kattex II		Ligex I		Ligex II	
Fatty acid	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Sum saturated	27.0	21.8	21.8	22.4	25.9	21.3	22.3	23.9	28.1	22.9	21.7	22.4
Sum branched	0.9	0.8	0.7	0.7	0.6	0.7	1.2	0.8	0.6	0.5	0.7	0.7
16:1(n–7)	2.0	1.9	1.2	1.1	2.4	1.6	1.5	0.3	0.7	0.7	0.8	0.6
18:1(n–9)	14.4	10.2	14.2	15.4	11.4	9.0	9.8	9.9	12.6	11.0	13.8	14.3
18:1(n–7)	5.4	5.0	3.8	4.1	3.8	3.6	4.2	4.9	3.2	3.0	2.2	2.8
20:1(n–13)	0.1	0.4	0.4	0.4	0.5	0.5	0.6	0.4	0.3	0.0	0.1	0.3
20:1(n–11)	0.2	0.0	0.6	0.4	0.1	0.1	0.3	0.1	0.3	0.4	0.1	0.1
20:1(n–9)	0.8	0.9	1.6	2.2	0.4	0.4	1.0	1.0	0.9	0.0	0.6	0.7
22:1(n–11)	0.4	0.3	1.6	0.8	0.2	0.2	0.2	0.2	0.1	0.0	0.2	0.1
22:1(n–7)	0.5	0.1	0.2	0.1	0.2	0.1	0.1	0.0	0.1	0.0	0.1	0.1
Sum monounsaturated	25.2	20.0	24.9	25.8	20.5	16.5	19.0	18.0	18.6	15.1	18.9	19.9
18:4(n–3)	0.6	0.5	0.2	0.3	0.3	0.2	0.2	0.3	0.8	1.0	0.4	0.3
18:2(n–6)	1.9	1.1	2.5	2.4	3.2	2.0	1.5	1.0	2.3	2.5	3.2	2.8
18:3(n–3)	0.7	0.4	0.7	0.7	0.6	0.5	0.3	0.1	1.3	1.6	1.0	0.9
20:4(n–6)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0
20:5(n–3) EPA	18.9	24.8	17.3	16.4	20.1	20.0	22.1	24.0	14.3	15.9	17.6	16.5
20:4(n–3)	0.6	0.5	0.6	0.7	0.6	0.6	0.4	0.5	0.6	0.6	0.6	0.4
21:5(n–3)	0.5	0.5	0.0	0.3	0.2	0.2	0.4	0.5	0.2	0.0	0.0	0.1
22:5(n–6)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0
22:6(n–3) DHA	22.5	28.8	29.7	29.0	26.9	37.1	30.6	29.5	32.4	36.3	35.0	34.8
22:5(n–3)	0.8	0.6	1.0	0.9	0.5	0.5	0.8	0.8	0.5	0.5	0.3	0.7
Sum polyunsaturated	46.8	57.5	52.6	51.1	53.0	61.5	57.4	57.4	52.7	61.4	58.7	57.0
Total 20:1 + 22:1	2.7	2.3	5.1	4.5	1.9	1.5	2.7	2.3	2.1	0.4	1.3	1.6

Note: Mean fatty acid values and only fatty acids mentioned in text are presented for clarity.

the Kattegat. Long-chain monounsaturated fatty alcohols in Ligurian zooplankton were 7% compared with 56–68% in Kattegat zooplankton (Table 5). There were negligible levels of alcohol detected in whole krill and faecal material.

The comparison of the three sites was achieved for both PL and TG fatty acids of whole animals using multivariate correspondence analysis to account for the covariation of the different fatty acid descriptors. Three axes were needed to explain 77 and 74% of the total inertia in PL and TG fatty acids, respectively.

For PL, the first axis clearly separates the Ligurian samples from samples of the other two sites (Fig. 1*a*), with C18 PUFA of the (n–3) family (dinoflagellate and other flagellate markers) as Ligurian descriptors and long-chain monoenoic acids such as 20:1(n–7) and 20:1(n–13) (copepod markers) as Clyde and Kattegat descriptors. The second axis showed a partial separation between Clyde and Kattegat samples, with Kattegat winter krill (male and females) as well as Kattegat summer female krill opposed to Clyde winter male and female and Clyde summer male krill (Fig. 1*a*). In terms of fatty acids, the second axis opposes the PUFA 20:5(n–3) and 22:6(n–3) to the C20 and C22 monoenoic acids. The hirerachical clustering based on the first five components (Fig. 1*b*) showed two major groups that characterised the PL from the Ligurian animals (C18 series, 22:6(n–3), 14:0, 18:0, 20:1(n–9), 20:1(n–11)) and from Clyde and Kattegat animals (C20 PUFA, acids from the (n–7) family, C21 PUFA, 16:0, 20:1(n–13), 22:1(n–9)).

TG fatty acids showed a similar pattern of separation on the first axis despite the influence of diet and despite having different fatty acid profiles compared with the PL (Fig. 2*a*). Here on the first axis, Ligurian populations are again separated from those of the other two sites. Interestingly, a certain degree of discrimination between males and females was observed during the reproductive seasons (Kattex I, Scotex I, and Ligex I) on axis 2, with reproductive females of all three sites being negatively defined on the axis. PUFA such as 18:5(n–3), 18:3(n–3), and 22:6(n–3) (flagellate markers) characterised the Ligurian side of axis 1, while 16:4(n–3), C21 PUFA, C20 PUFA, and C22 PUFA monoenoic acids (diatom and copepod markers) described the Clyde–Kattegat side of the same axis. The separations on the second axis are related to the opposition between C20 and C22 monoenes versus C16 and C18 monoenes. The hierarchical clustering showed three main groupings (Fig. 2*b*): in the first group, 20:1(n–9), 22:1(n–11), 16:4(n–3), and 20:5(n–3) (copepod and diatom markers) were associated with the Clyde winter populations; in the second group, C18 PUFA, C16 monoenes, 22:6(n–3), and most saturates were associated with the Ligurian samples, 18:5 and 22:6 (dinoflagellate and other flagellate markers) with summer samples, and 18:4, 18:3, 16:1(n–13)*t*, and saturates (flagellate and general phytoplankton markers) with winter females; in the third group, monoenes, 16:1(n–7), and 18:1(n–5) were associated with winter Kattegat females and the remaining C18, C20, and C22 monoenes (mixed diatom and copepod markers) with the other samples from both the Clyde Sea and the Kattegat.

Discussion

Nutritional status of *M. norvegica*

Lipid levels are a direct reflection of the physiological and

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Table 4. Percent composition (mean ± SD) of selected fatty acids in mixed zooplankton and *M. norvegica* faecal pellets sampled during the night from the Kattegat and the Ligurian Sea.

	Mixed zooplankton			Faecal pellets	
	Kattegat (N = 3)	Kattegat (N = 3)	Ligurian Sea (N = 1)	Kattegat (N = 1)	Ligurian Sea (N = 1)
Depth (m)	5–30	55–80	0–100		
Total lipid (% wet weight)	3.3±0.6	1.6±1.2	3.8	1.4	1.1
Sum saturated	27.4±3.3	30.4±7.4	20.5	40.6	12.3
*i*15:0	0.1±0.0	0.5±0.3	0.4	0.3	1.2
15:1	0.7±0.0	1.3±1.2	0.2	0.3	0.0
16:1(n–9)	0.2±0.0	0.1±0.0	0.2	1.0	0.5
16:1(n–7)	5.4±1.2	8.3±2.8	5.4	1.7	2.8
16:1(n–5)	0.4±0.0	0.8±0.2	0.3	1.7	0.0
18:1(n–9)	3.4±1.9	4.2±1.8	12.3	13.9	12.5
18:1(n–7)	1.3±1.7	1.0±0.6	2.4	5.2	2.1
18:1(n–5)	0.3±0.0	0.6±0.3	0.0	0.0	0.4
20:1(n–11)	1.4±0.6	0.1±0.6	0.1	0.4	0.0
20:1(n–9)	1.1±1.2	1.0±0.5	0.1	0.3	0.0
22:1(n–9)	0.9±0.3	0.1±0.5	0.0	0.0	0.0
Sum monounsaturated	17.4±11.1	18.8±12.0	21.3	25.1	21.7
16:4(n–3)	0.9±0.1	1.9±1.3	0.7	0.0	0.0
18:5(n–3)	0.3±0.4	0.2±0.0	0.5	0.0	0.0
18:4(n–3)	5.8±2.4	7.8±1.5	11.9	0.3	0.0
18:2(n–6)	1.7±1.3	1.5±1.1	2.6	16.3	19.8
18:3(n–3)	1.6±2.5	1.4±0.2	3.7	0.0	0.0
20:5(n–3) EPA	19.2±3.5	17.9±5.2	14.1	6.2	2.5
20:4(n–3)	0.9±1.2	0.9±0.5	2.6	0.0	0.0
21:5(n–3)	0.5±0.2	0.4±0.3	0.7	0.0	0.0
22:6(n–3) DHA	21.9±5.2	17.1±5.8	20.4	10.4	4.8
22:5(n–3)	0.7±0.8	0.6±0.0	0.3	0.0	0.0
Sum polyunsaturated	54.3±15.7	49.8±14.1	57.5	60.4	61.2
Total 20:1 + 22:1	3.9±6.8	2.4±0.0	0.6	1.1	0.0

nutritional status of an animal and can be influenced by the prevailing environmental conditions prior to sampling. Although season did not significantly influence lipid content in *M. norvegica* in this study, major differences associated with season have been reported in *M. norvegica* sampled from other areas (Falk-Petersen et al. 1981).

TG levels are usually determined by feeding activity and food supply. High levels of TG were found in krill from the Clyde Sea, which would indicate that there is a constant supply of food in this region throughout the sampling periods. This finding was also supported by high chlorophyll levels in this area (Mayzaud et al. 1998). Krill from the Clyde Sea during these periods also had higher numbers of copepod mandibles per stomach and higher stomach fullness levels compared with krill from the other sites (Lass et al. 2000). Mean TG levels were significantly lower in the Ligurian population compared with levels in krill from the Clyde Sea and the Kattegat (Mayzaud et al. 1999), which is consistent with the more oligotrophic conditions in the Ligurian Sea.

Diet of *M. norvegica*

Fatty acids can be used as food chain markers, and feeding experiments have been conducted to verify the incorporation of specific dietary fatty acids into zooplankton lipids (Harvey et al. 1987; Virtue et al. 1993*b*; Graeve et al. 1994). Graeve et al. (1994) conducted feeding studies using copepods fed on diets of either diatoms or dinoflagellates in which incorporation of dietary fatty acids was clearly demonstrated. Limited studies have been conducted on the transfer of specific lipids through several trophic levels. Fraser et al. (1989), in laboratory experiments, described the transfer of fatty acids from phytoplankton through to zooplankton and then to herring. They reported this technique to be of limited use as a quantitative or even qualitative indicator of larval feeding. This technique is obviously dependent on information available on the lipid profiles of potential dietary prey. To a certain extent, phytoplankton-derived fatty acids may be passed up the food chain to euphausiids via copepods. Mayzaud et al. (1999) suggested that fatty acid tracers in omnivorous species should be present at concentrations higher than 1% of the fatty acids; below this level, the tracer is likely to be derived from ingested grazers.

Although no single fatty acid is specific for any one organism, a C16 and C18 PUFA mixture may be a characteristic feature of diatom or dinoflagellate fatty acid profiles, respectively. The major fatty acids in diatoms include the mixture of 16:1(n–7), C16 PUFA, and 20:5(n–3) (Dunstan et al. 1994). The major fatty acids present in dinoflagellates include the mixture of 18:4(n–3), 18:5(n–3), and 22:6(n–3) (Harrington et al. 1970; Mayzaud et al. 1976). The fatty acid 18:4(n–3) is typically also found in phytoplankton species other than diatoms, including various flagellates (Graeve et al.

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Table 5. Percent composition (mean ± SD) of fatty alcohols in mixed zooplankton sampled at night from the Kattegat and the Ligurian Sea.

	Mixed zooplankton		
	Kattegat (N = 3)	Kattegat (N = 3)	Ligurian Sea (N = 1)
Depth (m)	5–30	55–80	0–100
Total alcohol (% total lipid)	15.4±2.1	9.3±1.5	9.7
14:0	3.4±0.5	1.9±0.8	0.6
15:0	0.5±0.1	0.5±0.7	0.9
16:0	16.9±2.3	13.3±2.9	82.8
17:0	0.3±0.0	0.2±0.0	1.2
18:0	1.1±0.8	0.7±0.1	3.3
Sum saturated	60.0±10.1	60.2±12.6	92.4
*a*15:0	0.6±0.1	0.8±0.6	0.3
16:1(*n*–7)	6.0±1.2	3.3±2.2	0.2
18:1(*n*–9)	4.6±0.9	3.6±1.5	2.8
18:1(*n*–7)	2.0±0.0	2.2±1.2	0.2
20:1(*n*–11)	0.5±1.2	0.3±0.0	0.0
20:1(*n*–9)	16.2±2.4	22.7±5.2	1.9
20:1(*n*–7)	0.9±0.0	1.0±0.3	0.0
22:1(*n*–11)	38.0±6.4	43.6±8.2	5.3
22:1(*n*–9)	0.7±0.3	0.1±0.1	0.1
24:1	0.8±0.0	0.5±0.0	0.7
Sum monounsaturated	69.7±12.4	77.3±18.7	11.2
18:5(*n*–3)	0.3±0.0	0.2±0.5	0.2
18:4(*n*–3)	5.8±0.5	7.8±0.9	7.8
18:2(*n*–6)	4.2±0.8	2.7±1.2	0.3
18:3(*n*–3)	2.3±0.4	1.7±0.6	0.1
Sum polyunsaturated	12.6±1.7	12.4±3.2	8.4
Total 20:1 + 22:1	56.3±10.3	67.7±13.8	7.3

Note: Fatty alcohols <0.5% in all samples are not reported.

1994). Tintinnids also have been reported to have high levels of C18 monounsaturated fatty acids and PUFA (Claustre et al. 1988).

We observed negligible to very low levels of the characteristic diatom and dinoflagellate mixture fatty acid profiles in the PL fraction of *M. norvegica*. Higher levels, however, were present in the TG fatty acid profiles, which may reflect recent feeding and hence reveal more about trophic interactions than PL or total lipid profiles. A diatom fatty acid marker, 16:4(*n*–3), was detected in the TGFA in Clyde Sea summer krill and Kattegat winter krill at levels higher than those found in other zooplankton analysed in this study. Another fatty acid, 16:1(*n*–7), found at high levels in diatoms and also in copepods feeding on diatoms (Graeve et al. 1994), was found at significantly higher levels in Kattegat and Clyde summer krill compared with Ligurian and Clyde winter krill. This trend was also confirmed by Lass et al. (2000), who found high levels of phytol, diatom fatty acid, and sterol markers in stomach content extracts of Clyde summer krill that coincided with very high chlorophyll levels in the water column during that cruise.

A general phytoplanktonic marker, 16:1(*n*–13)*t*, was detected in Ligurian and Kattegat samples. Ligurian summer krill had significantly higher levels of the dinoflagellate–Haptophycae marker 18:5(*n*–3), which was also reflected in krill digestive gland fatty acid profiles (P. Virtue, unpublished data). This dinoflagellate–Haptophycae marker was detected in the Ligurian zooplankon sample at levels three times lower than in krill. Levels of 18:4(*n*–3), found in tintinnids and various nondiatom species such as *Phaeocystis*, were significantly higher in zooplankton than in krill. This nondiatom marker diminished through the trophic chain, a finding that may indicate specific species consumption by zooplankton only, possibly due to size or behavioural characteristics.

Flagellates are important dietary components of Ligurian krill whereas Kattegat and Clyde krill tend to rely more on diatoms either directly or on a secondary level through dietary zooplanktonic species (Mayzaud et al. 1999; Lass et al. 2000). Low 16:1/16:0 ratios were found in the TGFA of Ligurian krill in the present study. This feature may be indicative of a dietary dinoflagellate predominance, while higher ratios found in Clyde and Kattegat krill suggest a diatom dietary influence. Dinoflagellates (and (or) other flagellates) have high levels of docosahexaenoic acid, (22:6(*n*–3) (DHA), compared with diatoms, while eicosapentaenoic acid, 20:5(*n*–3) (EPA), is a major component of diatom fatty acid profiles (Mayzaud et al. 1976; Dunstan et al. 1994). Levels of DHA in the Ligurian krill were significantly higher (by two to three times) than EPA in the TGFA. Conversely, both Kattegat and Clyde krill had higher levels of EPA than DHA. This trend was also evident in the zooplankton samples in the Ligurian Sea and the Kattegat.

Meganyctiphanes norvegica relies heavily on copepods as a major dietary component at times. High levels of 20:1 and 22:1 fatty acids were found in the TG profile, particularly in winter (9–17%). Both 20:1 and 22:1 fatty acids and alcohols are found in some copepods and can make up 20 and 70%, respectively, in some species (Graeve et al. 1994), although levels can vary significantly with season in some species (Kattner et al. 1981). These fatty acids are not usually present in phytoplankton and are not detected in herbivorous krill species such as *Euphausia superba* (Virtue et al. 1993*a*, 1993*b*) and *Thysanoessa macrura* (Phleger et al. 1998). Carnivorous krill such as *Euphausia tricantha*, however, have high levels of these fatty acids (Phleger et al. 1998).

From the levels of 20:1 and 22:1 fatty acids, our results suggest that *M. norvegica* relies heavily on copepods in the Kattegat and Clyde Sea. Stomach content analysis by microscopy of *M. norvegica* from the same study area showed that copepods including species such as *Temora longicornis*, *Pseudocalanus elongatus*, and *C. finmarchicus* constituted a major component of the diet in both the Clyde Sea and Kattegat animals (Lass et al. 2000). Mixed zooplankton samples analysed in the present study, which were composed mainly of copepods but also included other crustacean species, had low levels of 20:1 and 22:1 fatty acids (1–4%). However, high levels of these long-chain monounsaturated fatty alcohols were found in the Kattegat zooplankton (56–68%) compared with the Ligurian zooplankton (7%). This situation where specific lipid compounds are found as either an acid or an alcohol but not both has been described in other copepods (Sargent and McIntosh 1974). Similar fatty acid and fatty alcohol profiles were also found in the stomach of *M. norvegica* sampled from the same study sites (Lass et al. 2000). *Meganyctiphanes norvegica* appears to totally catabolise the fatty alcohols of its prey species. This is

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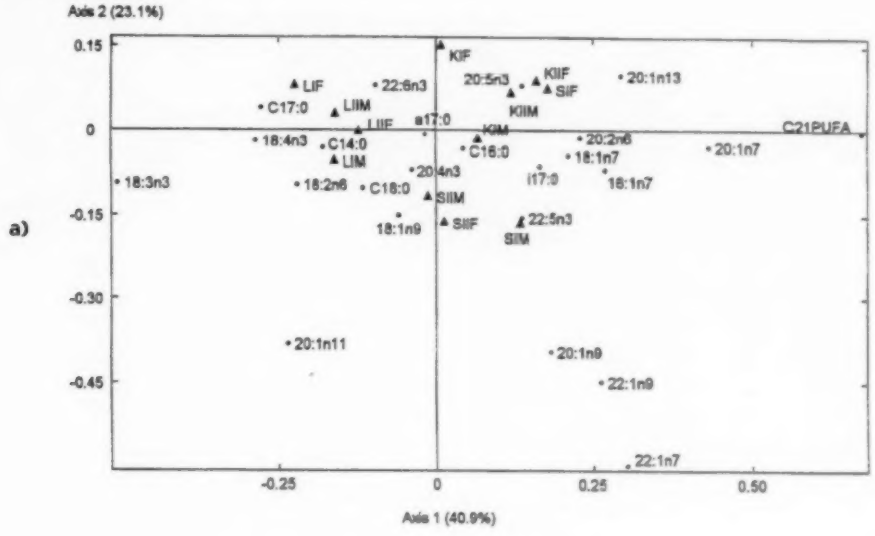
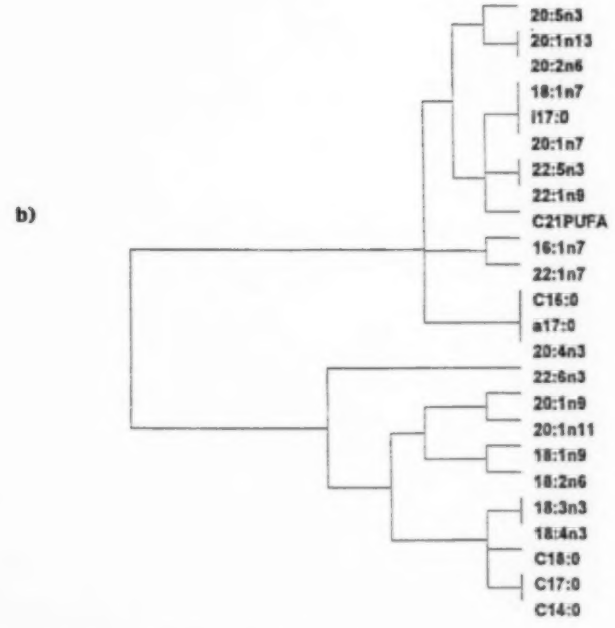
Fig. 1. Correspondence analysis of the PL fatty acids of whole male and female *M. norvegica* from Clyde Scotex I (SIM, SIF) and Scotex II (SIIM, SIIF), Kattegat Kattex I (KIM, KIF) and Kattex II (KIIM, KIIF), and Ligurian Ligex I (LIM, LIF) and Ligex II (LIIM, LIIF) during winter (SII, KII, LI) and summer (SI, KI, LII). (*a*) Projection of fatty acid descriptors and cruises; (*b*) dendrogram of hierarchical clustering of fatty acids.





also evidenced by the lack of wax esters in whole-body analysis in this species.

Krill from the Ligurian Sea had significantly lower levels of these long-chain monounsaturated markers. Zooplankton from the Ligurian Sea also had very low levels of these compounds. Very high levels of saturated alcohols (92% total alcohol) were present in the zooplankton, which were not found in lipid profiles of either stomach or whole-body analysis of krill. These results emphasise the fact that the fatty acid and alcohol composition of potential prey items must be well characterised before trophic relationships can be identified. The use of long-chain monounsaturated fatty acids and alcohols as copepod markers in the Mediterranean food web needs further investigation, particularly at the individual species level.

Levels of PUFA in PL varied with reproductive status. Significantly higher levels of PUFA were found in PL in reproductive female krill compared with male and female krill

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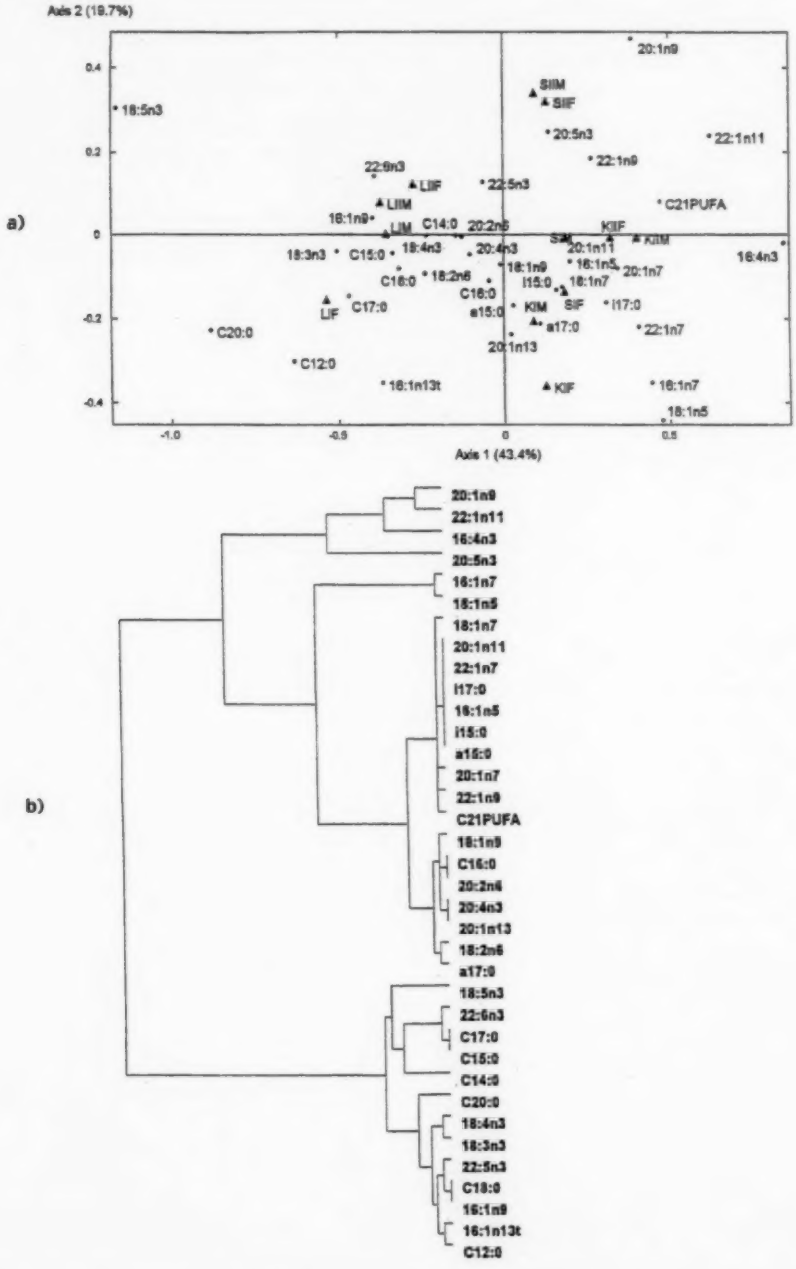
Fig. 2. Correspondence analysis of the TG fatty acids of whole male and female *M. norvegica* from Clyde Scotex I (SIM, SIF) and Scotex II (SIIM, SIIF), Kattegat Kattex I (KIM, KIF) and Kattex II (KIIM, KIIF), and Ligurian Ligex I (LIM, LIF) and Ligex II (LIIM, LIIF) during winter (SII, KII, LI) summer (SI, KI, LII). (*a*) Projection of fatty acid descriptors and cruises; (*b*) dendrogram of hierarchical clustering of fatty acids.



in the nonreproductive season. Conversely, significantly lower levels of PUFA in the TG fraction were found in reproductive female krill compared with male and female krill in the nonreproductive season. Most of the PUFA comprised the ω-3 fatty acids DHA and EPA, which constitute predominantly membrane lipids. Vitellogenic krill (female krill with developed ovary) appear to be preferentially channelling PUFA from the TG fraction to the polar fraction. Ovarian development requires additional membrane structural components for synthesis of egg membranes. High levels of PL are found in the ovary (Cuzin-Roudy et al. 1999). Additional PUFA may also be associated with the development of the fat

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body structure found in vitellogenic krill (Cuzin-Roudy and Buchholz 1999), which also has high PL levels.

Faecal pellet production is of interest both in physiological studies (Clarke et al. 1988) and in the role that zooplankton plays in the vertical flux of biogenic material into ocean sediments (Tanoue and Hara 1986). The organic composition of faecal material can provide information on the energy transfer process in food webs. There were marked changes in the relative composition of fatty acids in krill (and zooplankton) compared with those found in the faecal material. The major difference was in the reduction of PUFA, particularly in the Ligurian faecal sample, and conversely, high levels of saturated compounds, which was similar to that found in faecal samples from *E. superba* (P. Virtue, unpublished data). These dietary PUFA are being selectively metabolised by krill, although not to the same degree as reported in copepods and other euphausiids. Although PUFA are reduced substantially, they are still present in the faecal material in the Kattegat sample (up to 17% of the total fatty acids), which may imply an excess of dietary PUFA. In the Ligurian faecal samples, on the other hand, far less PUFA (7%) was present, which may be a consequence of the oligotrophic conditions in this area, while comparatively nutrient rich waters are found in the Kattegat. High levels of 18:0 were reported in copepod faecal pellets compared with their dietary sources, and PUFA levels were reduced to very low or trace levels (Harvey et al. 1987; Neal et al. 1986).

Surprisingly high levels of 18:2(n–6) were found in faecal material (16–20%) compared with 1–3% in whole-body and zooplankton samples (1–3%). This finding has not been reported previously. Significantly higher levels of 18:2(n–6) have been found in the cell wall extracts of *Nannochloropsis*, a cosmopolitan eustigmatophyte alga, compared with the whole-cell extracts (P. Mansour, CSIRO, G.P.O. 1538, Hobart 7001, Tasmania, Australia, personal communication). Algal cell walls may be more resistant to digestive enzymatic processes in krill. Alternatively and similar to saturated compounds, 18:2(n–6) may be an excess product of either fatty acid metabolism or the elongation and desaturation process. The high levels of 15:0 and 17:0 found in the faecal material may be indicative of bacterial breakdown during the degradation process. Although analysis was limited in this study to two samples, faecal fatty acid profiles may help us understand fatty acid metabolic pathways and the nutritional requirements of krill. This approach, although limited in terms of use as dietary markers, warrants further investigation.

Correspondence analysis clearly identified the Ligurian population as different from the other two, for both the PL and the dietary-influenced TG. Dinoflagellate and other flagellate fatty acid mixtures (C18 PUFA of the (n–3) family), being Ligurian descriptors, were responsible for this separation. Copepod fatty acid mixtures ((20:1(n–7) and 20:1(n–13)) and diatom fatty acid mixtures were responsible for the separation of the Clyde and Kattegat populations from the Ligurian population.

Partial discrimination of the Clyde and the Kattegat communities was obvious from PL but not from TG fatty acids. Long-chain ω-3 fatty acids and long-chain monounsaturated fatty acids were responsible for this partial separation. This may suggest that the krill in Kattegat are more carnivorous than those in the Clyde Sea, which correlates with the higher ratio of copepod to phytoplankton biomass found in the Kattegat compared with the Clyde Sea (Lass et al. 2000).

The correspondence analysis revealed a distinction between male and female neutral lipids in the reproductive seasons. The neutral lipids were obviously more influenced by the physiological status of the animal, probably related to the nutritional requirements for egg production. PUFA levels in PL also vary significantly with reproductive status, emphasising the role of these membrane compounds in egg production.

In conclusion, *M. norvegica* adapts to diverse environmental conditions partly due to its ability to physiologically cope with a variable food and temperature regime. In terms of TG and PL fatty acid profiles, the Ligurian populations are statistically separated from the Kattegat and Clyde populations. The Clyde and the Kattegat populations are separated from each other in terms of PL fatty acid profiles only. Krill are predominantly carnivorous in the Kattegat, and the Ligurian and Clyde populations rely more on phytoplanktonic material in the diet. At times, copepods are a major component in the diet of *M. norvegica* in all areas.

Lipid and fatty acid profiles have revealed between- and within-site differences in the krill *M. norvegica*, an important component of the northern hemisphere food webs. At the present time, it appears to be difficult to separate transfer between primary and secondary trophic levels, and we consider this an important area for future research.

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Metabolic and enzymatic adaptations in northern krill, *Meganyctiphanes norvegica*, and Antarctic krill, *Euphausia superba*

Friedrich Buchholz and Reinhard Saborowski

Abstract: The Antarctic krill, *Euphausia superba*, is restricted to the Antarctic Ocean. The northern krill, *Meganyctiphanes norvegica*, is extremely widely distributed from the arctic North Atlantic to the warm Mediterranean. Respiration measurements showed no seasonal differences in rates determined in krill from the thermally stable Clyde Sea (Scotland) and the cooler but variable Danish Kattegat. In the warm Ligurian Sea, where temperatures are stable, krill showed higher rates in April than in September, indicating reactions to the short but intensive productive season. Krill can passively benefit from enhancements of overall metabolism when ascending into upper, warmer water strata during their pronounced diel vertical migration. Michaelis–Menten constants (K_m) of citrate synthase (CS) were compared. In terms of respiration and enzyme regulation, krill from the Ligurian Sea stand apart: temperature and nutrition appear to be of different influence, relatable to genetic differentiation in the species. In contrast, K_m of CS in *E. superba* is temperature independent, highlighting the species' stenothermal physiology. A basal level of activity of digestive enzymes ensures immediate utilization of patchy food sources. Specific induction, including that of chitinases, indicating omnivory in both species, underlines krill's exceptional capacity to adapt to highly variable trophic environments. Processes of moult, growth, and reproduction are locally and seasonally adjusted.

Résumé : Le krill antarctique, *Euphausia superba*, n'habite que l'Océan antarctique, alors que le krill nordique, *Meganyctiphanes norvegica*, possède une répartition géographique très étendue qui va de la région arctique de l'Atlantique Nord aux eaux chaudes de la Méditerranée. Les taux respiratoires n'accusent pas de variation saisonnière chez le krill de la mer de Clyde en Écosse, un milieu à forte stabilité thermique, ni chez celui du Cattégat danois, une mer plus froide et plus changeante. Dans la mer Ligurienne, où les températures sont chaudes et stables, le krill a des taux respiratoires plus élevés en avril qu'en septembre, en réaction à la courte mais intense saison de production. Le krill peut bénéficier passivement d'un accroissement général de son métabolisme lorsqu'il se déplace vers les couches d'eau supérieures plus chaudes durant sa migration verticale quotidienne marquée. Nous avons comparé les constantes de Michaelis–Menten (K_m) de la citrate synthase (CS). En ce qui a trait à la respiration et la régulation enzymatique, le krill de la mer Ligurienne fait bande à part: la température et la nutrition semblent y avoir une influence particulière, à cause d'une différentiation génétique chez l'espèce. En revanche, la K_m de la citrate synthase est indépendante de la température chez *E. superba*, une caractéristique physiologique d'une espèce sténotherme. Le maintien d'un niveau d'activité de base chez les enzymes digestives permet l'utilisation immédiate de ressources alimentaires à répartition contagieuse. L'induction spécifique, entre autres celle des chitinases, qui indique l'omnivorie chez les deux espèces, illustre l'extraordinaire capacité du krill à s'adapter à des environnements trophiques extrêmement variables. Les mécanismes de la mue, de la croissance et de la reproduction s'adaptent aux conditions locales et saisonnières.

[Traduit par la Rédaction]

Introduction

The northern krill, *Meganyctiphanes norvegica*, attains the largest body size among the euphausiid species of the northern hemisphere. Its distribution covers an exceptionally wide longitudinal and latitudinal range in North Atlantic waters, spanning from the Gulf of St. Lawrence to the Aegean Sea and from the Barents Sea to the upwelling zones of the Cape Verde Islands (Mauchline and Fisher 1969). Accordingly, this krill species is ideally suited for a model study in climatic adaptation.

Based on earlier work on local populations of *M. norvegica*, comparative investigations in the framework of the Third Marine Science and Technology Programme of the European Union were conducted in three areas during 1996–1999 (Buchholz et al. 1998). The Ligurian Sea in the warm and constant northern Mediterranean Sea and the Clyde Sea, which reflects cool and constant Atlantic conditions, were contrasted by the Danish Kattegat where waters of the North and Baltic seas meet with consequently variable temperatures.

This study concentrates on results of the project and earlier literature in terms of ecophysiological climatic adaptation, traced by respiration measurements, and the characteristics of key metabolic and digestive enzymes. These are discussed

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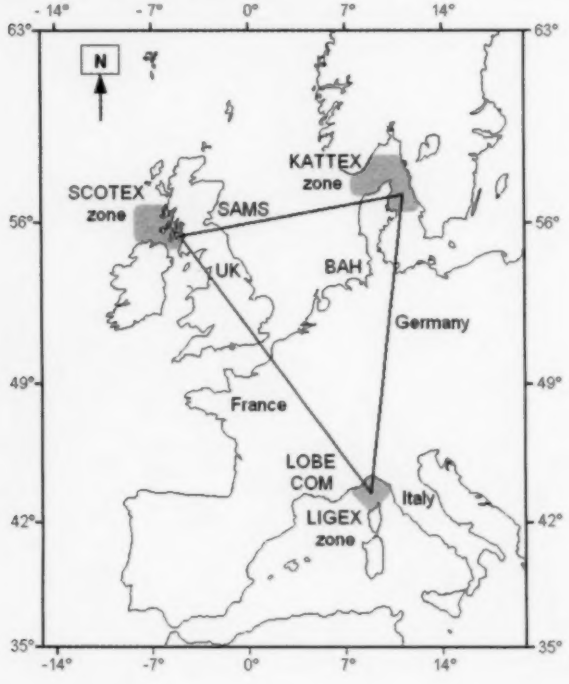
Table 1. Locations and sampling periods.

Location	Cruise	Season	Position	Max. depth (m)	Sampling period
Ligurian Sea	Ligex I	Winter–spring	43°00′N, 07°30′E	2000	1–29 April 1996
	Ligex II	Summer–fall			5–25 Sept. 1997
Clyde Sea	Scotex I	Summer–fall	55°40′N, 05°00′W	150	2–11 July 1996
	Scotex II	Winter–spring			15–28. Feb. 1997
Kattegat	Kattex I	Summer–fall	57°18′N, 11°25′E	131	14–29 July 1996
	Kattex II	Winter–spring			4–19 March 1997

Fig. 1. Climatic triangle. Source: PEP database (physiological ecology of a pelagic crustacean).



in the light of the multidisciplinary approach on population dynamics and behaviour (Guérin-Ancey et al. 1998; Tarling et al. 1998*b*, 2000) and on adaptive processes linked to nutrition (Lass et al. 2000; Virtue et al. 2000), reproduction (Cuzin-Roudy and Buchholz 1999; Cuzin-Roudy 2000), and lipid metabolism (Mayzaud et al. 1999), including the first attempt to differentiate a possible genetic separation of these populations (Zane et al. 2000).

Meganyctiphanes norvegica is an exceptionally strong vertical migrator. Accordingly, when krill energetics are discussed, these have to be related to different regimes with a spring amplitude of diel vertical migration (DVM) of 800 m in the deep Mediterranean (Velsch 1997) as well as less than 100 m at the shallower northern locations (Tarling et al. 1998*a*). Different effects of the local seasonal trophic regimes are also taken into account where applicable.

In contrast with *M. norvegica*, the Antarctic krill, *Euphausia superba*, is strictly bound to polar waters. With respect to adaptive features of respiration and enzymes, some comparisons will be drawn with the largest and most numerous euphausiid on the basis of recent work, particularly under seasonal aspects. Finally, some open questions in krill ecophysiology will be highlighted and possible ways to find answers to these by multidisciplinary approaches.

Euphausiid metabolism

Meganyctiphanes norvegica in the climatic triangle: locations, hydrography, and trophic conditions

Locations

For the biological comparison, locations (see Fig. 1) were chosen where abundant swarms of krill had been regularly encountered and studied previously: the Arran Deep in the Clyde Sea, western Scotland (Mauchline 1960), the Läsö Deep in the Danish Kattegat (Buchholz and Boysen-Ennen 1988), and the frontal system in the Ligurian Sea, which was located at the beginning of the cruises by conductivity–temperature–depth sonde (CTD) on a section between Nice and Calvi (Corse) (Labat and Cuzin-Roudy 1996).

The cruises (Table 1) were conducted onboard the German RV *Heincke*, a 1990-built, 1000-t, multipurpose ship. The CTD, an acoustic doppler current profiler (ADCP, 150 kHz), a dual-frequency sonar (38 and 120 kHz), and a multi-opening/closing net system with an environmental sensing system (MOCNESS, 1 m^2, 300- and 2000-μm mesh) were regularly deployed and maintenance experiments with live krill performed in parallel.

Hydroclimatic features

A review of the situation encountered during at least one cruise in winter and summer to the Clyde Sea and the Kattegat is given in Matthews et al. (1999). Here, the measurements made during the cruises are related to general oceanographic features of the areas. Another covering the Ligurian Sea is currently being prepared. In the present paper, typical thermal profiles from the climatic triangle are presented as a background for biological adaptation (Fig. 2).

The subsurface and deep waters (>2000 m) of the Ligurian Sea are constantly at 12–13°C during summer and winter, while only a thin surface layer (about 30 m) increases in temperature during summer (up to 24°C). During vertical migration, krill enter the surface layers only for short periods but generally remain below a sharp thermocline at about 30 m (Tarling et al. 1999*a*).

The Scottish Firth of Clyde is colder than the Ligurian Sea. In the Arran Deep, winter temperatures were constantly at 6–8°C throughout the water column. During summer, a slight stratification appeared with warmer surface waters of up to 12°C. However, krill were again exposed to comparatively constant diel and annual temperatures.

In sharp contrast with these conditions, the Danish Kattegat is characterized by high thermal variability. The

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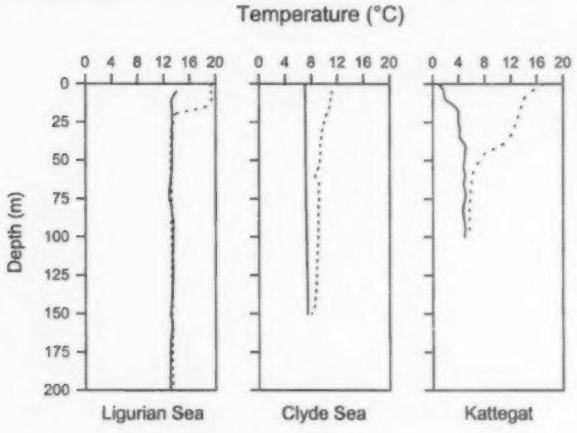
Table 2. Chlorophyll *a* (Chl *a*) concentrations integrated over a 100-m water column (Chl *a* determined on filters by fluorometry) and energy values of krill stomach contents (converted from carbon, hydrogen, and nitrogen analysis after Salonen et al. (1976); n = 6–12 krill).

	Ligurian Sea		Clyde Sea		Kattegat	
Season	Chl *a* ($\mu g \cdot m^{-2}$)	Energy ($J \cdot individual^{-1}$)	Chl *a* ($\mu g \cdot m^{-2}$)	Energy ($J \cdot individual^{-1}$)	Chl *a* ($\mu g \cdot m^{-2}$)	Energy ($J \cdot individual^{-1}$)
Winter–spring	38–181 (Apr.)	2±1	10–33 (Feb.)	3±2	21–96 (Mar.)	2±1
Summer–fall	27–31 (Sept.)	1±1	317–422 (July)	5±4	24–32 (July)	2±1

Note: Source: P. Mayzaud (Laboratoire d'Océanographie Biochimique et d'Ecologie, Observatoire Océanologique, B.P. 28, 06230 Villefranche-sur-Mer, France, personal communication) and R. Saborowski (PEP database, personal communication).

Fig. 2. Thermal profiles during summer (broken line) and winter (solid line) from CTD measurements. Source: PEP database.



summer surface temperatures of the Kattegat reached 16–18°C. With depth, temperature decreased continuously towards 6–8°C due to stratification brought about by a northward flow of near-surface Baltic water, which is very cold in winter and heated considerably during the summer, and southward-flowing cool North Sea/Skagerrak water at depth. During the winter, surface temperatures fell below 2°C but increased gradually toward the bottom to about 5°C. Accordingly, within the range of DVM, krill may be exposed to shifts of temperature of up to 8°C. Seasonal variation may even exceed 12°C.

Trophic conditions

The trophic environments at the three locations are distinctly different. Recent results underline that *M. norvegica* is an opportunistic feeder and feeds on both phyto- and zooplankton (Bamstedt and Karlson 1998; Onsrud and Kaartvedt 1998). A thorough comparison of food sources in the water columns of the Clyde Sea and Kattegat and food selection by stomach contents analysis is given in Lass et al. (2000) and by lipid analysis in Virtue et al. (2000).

To concisely characterize the seasonal feeding conditions, chlorophyll *a* (Chl *a*) values are given in Table 2. Due to the complexity of food selection in krill, the energy content of the material ingested, irrespective of its source, was determined by carbon, hydrogen, and nitrogen analysis (Salonen et al. 1976) of stomach contents. These values are presented to illustrate seasonal variability in food and feeding conditions at the three sites.

To complement these "snapshot" descriptions of trophic situations encountered during the cruises, the annual course of nutritional conditions is further characterized. In the Ligurian Sea, the productive months are limited in time and only last from mid-March to the end of May. Otherwise, this area and the whole Mediterranean are typically oligotrophic (Fabiano 1984; Goffart et al. 1995). These conditions are reflected in the above values.

In the Clyde Sea, in contrast, feeding conditions are favourable, with a long period of high production: April–October (Gowen et al. 1998). During the winter cruise, both phyto- and zoo-plankton standing stocks were low, i.e., corresponded to a food-depleted winter situation.

In the Kattegat, phytoplankton levels are always low and bound to the surface layer that krill usually do not enter during DVM. However, krill rely strongly on copepods, these being advected from the Baltic and the deep Skagerrak currents (Buchholz et al. 1995). As a consequence, a long phase of enhanced production or availability of plankton lasts from April to November (Buchholz and Boysen-Ennen 1988). The winter–summer difference during the cruises was not pronounced.

Meganyctiphanes norvegica in the climatic triangle: adaptations in respiration and enzymes

Respiration

Measurement of oxygen consumption is problematic in planktonic and pelagic species. Accordingly, in order to avoid a major shortcoming, a measuring chamber was designed to prevent krill from being influenced strongly by confinement (Fig. 3). Details are given in Saborowski and Buchholz (1998).

A slow, upward-directed, and circular current was generated in the chamber. This helped the specimens to stay clear of the bottom and orient themselves to swim against the constant current. Natural swimming behaviour in krill was thus encouraged, particularly preventing krill from contacting the chamber walls too frequently.

Six chambers were immersed in a temperature-controlled water bath. One served as control. The others were equipped with two to five specimens in order to reduce individual variation. Only male krill were used to generate a reliable data set (n = 4–14 per data point per temperature), and respiration measurements were normalized to a 30-mm standard krill.

In an intersite comparison (Fig. 4), the oxygen consumption rates ranged between 20 and 90 $\mu mol\ O_2 \cdot mg\ dry\ weight^{-1} \cdot h^{-1}$ and followed exponential relationships with experimental temperatures between 4 and 16°C, corresponding to the predominant natural range that *M. norvegica* encounters. In Clyde and Kattegat krill, almost no seasonal varia-

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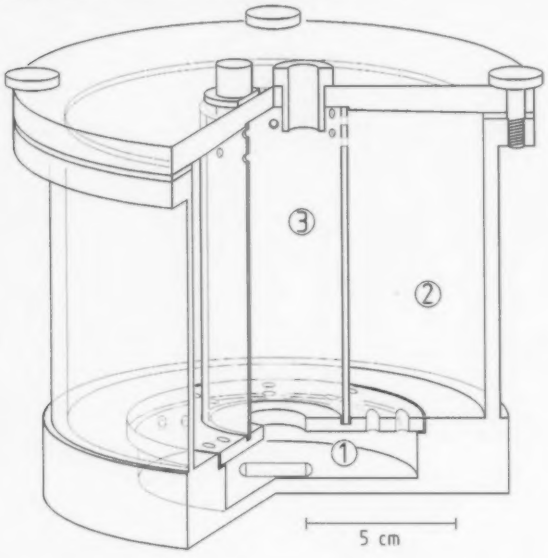
Fig. 3. Respiration chamber with self-generating current system. 1, current generator; 2 and 3, outer and inner cylinder, respectively. Source: Saborowski and Buchholz (1998).



tion exists in respiration. Summer–fall values (September) in Ligurian krill overlap to a large extent with the respiration curves of krill from the other two locations. The exception is winter–spring respiration in the Ligurian krill. Here, all values are enhanced by at least 80% in relation to summer values. Winter–spring values (April) in Ligurian krill and summer values in Kattegat krill (July) were confirmed by repetition of the experiments (data not shown).

Firstly, relationships to seasonal temperature adaptation are considered. The thermal winter–summer differences in the Clyde Sea are small and could explain the lack of seasonal adjustments of overall rates. However, the high thermal variability in the Kattegat should then cause an overall adaptive shift in rates. This is apparently not the case. However, respiration rates in the Clyde Sea were consistently 20–30% lower when compared with those in the Kattegat. This may be interpreted as a thermal adaptation: a range of 30–35 µmol O_2·mg dry weight^{-1}·h^{-1} (highlighted by horizontal bars in the graphs) corresponds to the annual mean temperature of 6–9°C in the Clyde Sea. The same range of oxygen consumption corresponds to 4–7°C in the Kattegat. This range equals the annual temperature amplitude in the deeper layers in the Läsö Deep (compare with the temperature range indicated above the abscissa in Fig. 4). Accordingly, the adjustment to the low temperature ranges encountered during most times of the year may be physiologically more important at both locations than the vertical temperature differential met during summer.

At the same time, at both sites, the thermal stratification in the water column, which develops most strongly in the Kattegat with a difference of about 10°C in summer, may be of physiological advantage with respect to DVM. An enhancement of the overall metabolic rate would be advantageous as krill crossed the thermocline: the rate increase with temperature may facilitate motility in the search for food and the ability to escape from predators. This may then be interpreted as a passive effect of metabolic enhancement because no short-term active adjustments to changing temperatures were apparent; such would have been detectable, e.g., as horizontal intersections in the respiration curves. In fact, respiration rates follow smooth exponential courses.

It is interesting to note that the range of 30–35 µmol O_2·mg dry weight^{-1}·h^{-1} equally corresponds to summer–fall respiration in the Ligurian krill at temperatures of 12–13°C prevailing below the thermocline, where krill remain for most of the time. Furthermore, when krill from all three sites are compared, the correspondence of this standard respiration rate of 30–35 µmol O_2·mg dry weight^{-1}·h^{-1} may be interpreted as an effect of metabolic temperature compensation (sensu Hochachka and Somero 1984). The overall respiration curves show vertical shifts and result in the same metabolic rate at the prevailing temperature at each site, i.e., at 12–13°C in the Mediterranean, 6–9°C in the Clyde Sea, and 4–7°C in the deep layers of the Kattegat.

However, winter–spring values in Ligurian krill are consistently more than 80% higher than summer–fall respiration at this site, corresponding to a vertical upward shift of the respiration curve. Most probably, seasonal trophic change plays a role in this respect.

In the Ligurian Sea, the very short period of elevated primary production begins in mid-March and usually ends in May (Goffart et al. 1995), providing the basis for intensive somatic growth and reproduction in krill. In fact, krill strongly rely on phytoplankton during that time (de La Bigne 1985). Males start to produce spermatophores continuously, while females go through vitellogenesis and several consecutive spawning events (Cuzin-Roudy 1993). Compared with the Clyde Sea and the Kattegat, Ligurian krill have by far the shortest reproductive period, which, moreover, is closely interlinked with the onset of phytoplankton production. Furthermore, DVM ranges are at their maximum (Velsch 1997), and high excretion rates were measured (Roger 1978). Apparently, during the spring period, physiological and behavioural changes occur that cause an exceptional increase in overall metabolic rates in Ligurian krill.

In summary, respiration as an expression of overall metabolism shows the following features: metabolic rates in krill from different climatic regions are adjusted to maintain a comparable level tuned to the prevailing temperature regime, passive use of the temperature differential in stratified waters may enhance physiological capacity during DVM, krill from the northern locations appear to be predominantly affected by temperature, and in the Mediterranean, trophic conditions are superimposed on temperature adaptation, linked to the short productive season in an otherwise oligotrophic sea. Generally, irrespective of the sites, short-term adjustments of metabolic rates did not occur. Accordingly, systematic, long-term environmental adaptation prevails.

Metabolic enzymes

Alongside the determination of overall metabolic capacity in live krill, physiological performance and adaptive capability were also studied with regard to key metabolic enzymes. Changes in enzyme kinetics or synthesis are directly related

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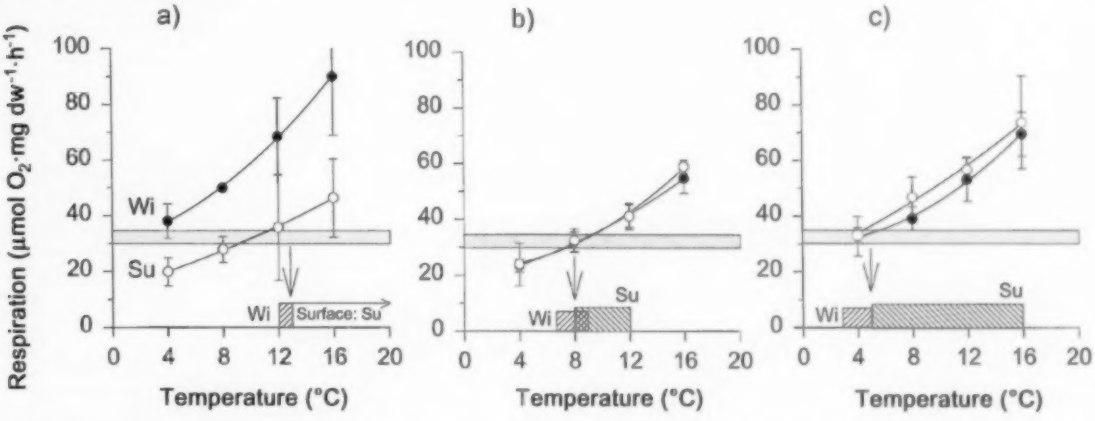
Fig. 4. Oxygen consumption in (*a*) the Ligurian Sea, (*b*) the Clyde Sea, and (*c*) the Kattegat normalized to a 50 mg dry weight (dw) krill (means ± SD, n = 6–10). Bars highlight respiration rates at ambient temperatures (see text); seasonal ranges are marked on the abscissa: Wi, winter; Su, summer. Source: R. Saborowski et al. (unpublished data) and Saborowski et al. (2000*a*). Method in Saborowski and Buchholz (1998).



to acclimation and adaptation to ambient temperatures, since enzyme activity is involved at all levels of metabolism (Clarke 1983). Citrate synthase (CS) is an enzyme instrumental in energy metabolism that has a control function in the citric acid cycle. Pyruvate kinase (PK), a regulatory enzyme of the glycolytic pathway, is involved in ATP production.

Work on CS and PK confirmed previous studies that showed that adjustments of the basic characteristics temperature maximum, energy of activation, and thermal stability are unimportant in temperature acclimatization in *M. norvegica* (Vetter and Buchholz 1997). Maintenance experiments showed, however, that the species adjusts specific activity of CS to different temperatures during acclimation over 11 days (Vetter 1995*a*).

Such a capacity to compensate thermal influences by maintaining a similar level of activity irrespective of the ambient temperature would be expected to play a role in longer term adjustments to seasonal temperature changes. The same compensatory mechanism might equally be involved as a response to short-term temperature changes that krill experience during DVM. However, determinations of specific activities in samples as compared at a standard assay temperature of 25°C taken from the climatic triangle during both seasons did not support this hypothesis (Saborowski and Buchholz 2000). The seasonal comparison resulted in nonsignificant changes of specific activity in the Clyde Sea and the Kattegat. Equally, CS activity remained at a similar level when samples taken from the field at different ambient temperatures at different depths following a daily cycle were analysed. Accordingly, quantitative enzyme regulation by adjusting specific activity to temperature appears unimportant at both seasonal and diel time scales. The same applies to the specific activities determined for PK (Salomon et al. 2000).

With respect to season, however, a significantly diminished value of specific activity (–25%) was found in krill taken during summer–fall (September) in the Ligurian Sea as compared with the activity in winter (April). Temperatures are the most uniform in the Ligurian Sea (Fig. 2). Accordingly, not the thermal influence but other factors must have caused the downscaling of CS activity during September. Here again, the strong seasonal contrast of the trophic environment may have been responsible for this effect.

Variability was apparent in specific activities in CS and PK determined in the abdominal muscle tissue in the seasonal samples from all three sites. When winter and summer values were paired and the proportional activity of CS/PK calculated, these proportions fell on a straight line with a negative slope when regressed against dry weight (y = –0.0053 + 0.3570; r^2 = 0.994). Apparently, a fixed ratio of CS/PK exists, indicating an allometric relationship where CS correlates negatively with weight and PK positively (details are given in Saborowski and Buchholz 2000). Such an effect is known as metabolic scaling (Childress and Somero 1990; Berges and Ballantyne 1991). PK-rich cells and thus activity simply increase with weight. With respect to CS, possibly the muscles fibres of the large abdominal muscle system are multiplied to a larger extent than the most active, mitochondria-rich, but small, ventrally situated pleopod muscles. Accordingly, the relative number of mitochondria decreases and thus CS activity.

Obviously, the seasonal differences found in the specific activities of PK and CS are attributable to metabolic scaling in krill, irrespective of their geographic origin, and depend on the size of the animals. However, as indicated above, the summer–fall (September) activity in the Ligurian krill was found to be considerably depressed. As a consequence, the CS/PK ratio deviated significantly (<50%) from the expected value calculated from the CS/PK regression. The depressed CS activity in summer krill in the Ligurian Sea may relate to the low food availability during the long oligotrophic phase. Possibly, somatic reduction takes place to save energy during food-limiting conditions.

An adjustment of specific activities to compensate for environmental effects, particularly temperature (or nutrition, see below), can be taken as an indication of quantitative enzyme regulation (Hochachka and Somero 1984). An alternative is the qualitative strategy, i.e., to modulate substrate

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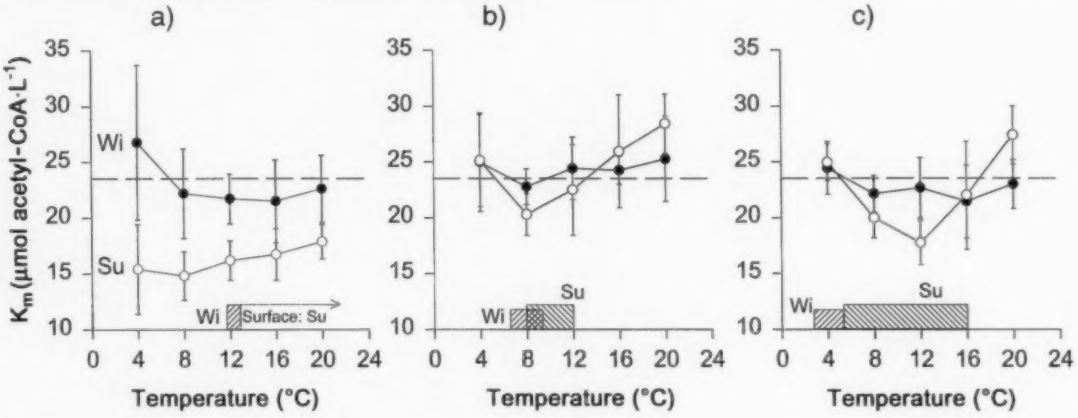
Fig. 5. Substrate affinity (K_m) towards acetyl-CoA of CS in relation to assay temperature from seasonal samples (n = 6–12) in (*a*) the Ligurian Sea, (*b*) the Clyde Sea, and (*c*) the Kattegat. The broken line marks the mean of all measurements, irrespective of site during winter. Seasonal temperature ranges are marked on the abscissa: Wi, winter; Su, summer. Source: R. Saborowski et al. (unpublished data) and Saborowski and Buchholz (2000). Methods in Vetter (1995*a*).



affinity. The Michaelis–Menten constant (K_m) is the common measure. A decrease in K_m corresponds to enhanced substrate affinity resulting in an increase in catalytic capacity and vice versa.

The determination of K_m is tedious and requires highly standardized procedures. An exceptionally large data set is needed to differentiate environmental influences. Here, it is assumed that the K_m determined at different assay temperatures in vitro reflects the changes due to structural adjustments of the enzyme in vivo. Values of K_m in CS were determined accordingly and compared under appropriate seasonal and geographic conditions.

During winter, the K_m values determined were very uniform at all three sites (Fig. 5). With little variation, all values followed nearly horizontal lines and are close to an overall average of 23 µmol·L^{-1} (broken line in the graphs). Apparently, no regulatory capacity via K_m exists during winter.

Firstly, this effect may correspond to the isothermal conditions of the water columns at the sampling locations without a need for thermal adjustment. Secondly, a fixed level of enzymatic turnover potential is maintained in CS, irrespective of the ambient temperatures, which are distinctly different at each site (Fig. 2).

Summer conditions appear to have pronounced effects on the course of K_m values. Most drastically, the complete curve is shifted to lower values in Ligurian krill. With respect to the prevailing ambient temperature of 12–13°C, substrate affinity is doubled at this location and results in a considerable gain of enzymatic turnover capacity.

In the Clyde Sea and the Kattegat, K_m curves were V-shaped. In the Kattegat, the K_m was significantly lowered by about 40% at a temperature of 12°C with respect to the corresponding winter value. In the Clyde Sea, the V-shape was generally less pronounced and showed a minimum at 8°C.

The winter–summer differences in K_m are partly unexpected with regard to common hypotheses of enzymatic adaptation. According to the reasoning of Baldwin (1971), Baldwin and Hochachka (1971), and Hochachka and Somero (1984), K_m adjustments of different metabolic enzymes are important in thermal adaptation. A suite of congeneric species, mostly fish from different latitudes, were compared as well as adaptation experiments conducted and later extended to invertebrates (e.g., Dahlhoff and Somero 1993; Vetter and Buchholz 1997). Generally, K_m values are adapted or "conserved" in different species so that K_m minima coincide with the ambient temperature range, particularly with emphasis on metabolic cold adaptation. Literature on seasonal adaptation is scarce, however. Vetter and Buchholz (1997) pointed out that a complex combination of adaptive mechanisms is needed to optimize metabolic enzymes under varying temperature regimes.

With regard to these considerations, adaptive traits of K_m variation in *M. norvegica* may be interpreted as follows. During winter, in spite of different ambient temperatures, the same level of substrate affinity is maintained at all three sites. This effect would correspond to metabolic temperature compensation. However, this is not expressed in the classically expected distinct K_m minima, which would be adjusted to the local prevailing temperatures of 12, 7, and 5°C.

In summer in the Ligurian Sea, the qualitative adjustment of K_m presumably compensates for the quantitative reduction in terms of specific activity in muscle CS. At the same time, the strong trophic influence on metabolism such as that found in respiration in an isothermal environment appears to be confirmed. In summer in the Kattegat, thermal adaptation appears to be influential: K_m is adjusted in such a way that the same K_m as that during winter applies when krill stay in the cool deep during daytime. When krill migrate up into the warm near-surface layers during nighttime, K_m is systematically lower by about 40%, resulting in enhanced enzymatic capacity. This effect would then also help to increase motility during foraging and escape. The same effect, although less pronounced, may apply to the Clyde Sea due to the weaker temperature differential during summer in these waters.

Digestive enzymes

In the frame of the European Union project, a suite of digestive enzymes were analysed as indicators of qualitative and quantitative selection of planktonic food organisms in

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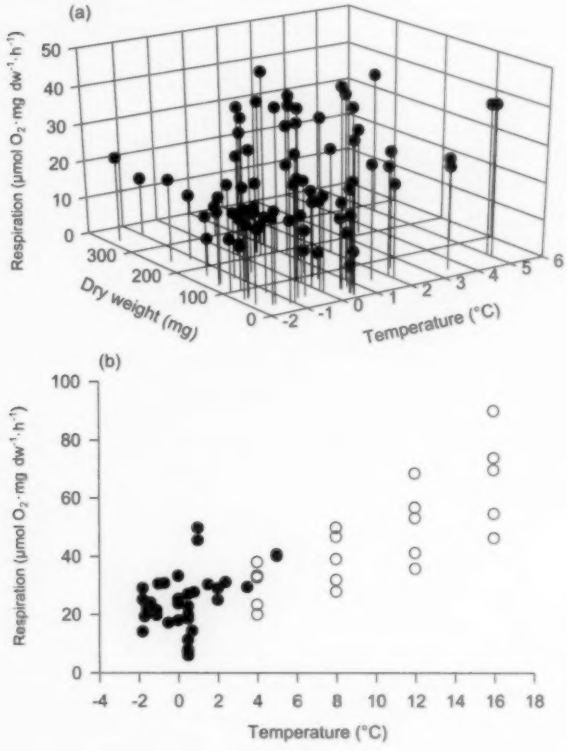
Fig. 6. (*a*) Respiration of *E. superba* related to body weight and temperature. Source: Opalinski (1991) and Torres et al. (1994). (*b*) Respiration rate of *E. superba* versus temperature (solid circles; single values of krill in the weight range of 20–100 mg dry weight; source as above) and *M. norvegica* (open circles; rates normalized to a 50 mg dry weight krill; averaged data; source: Saborowski et al. 2000*a*).



M. norvegica. Results show a high potential of enzyme induction associated with sources of nutrition of both phyto- and zoo-plankton origin. Furthermore, K_m variation with temperature exists. The opportunistic behaviour in food selection (Bamstedt and Karlson 1998; Lass et al. 2000) is reflected in the repertoire and regulation of digestive enzymes. P. Mayzaud et al. (Laboratoire d'Océanographie Biochimique et d'Ecologie, Observatoire Océanologique, B.P. 28, 06230 Villefranche-sur-Mer, France, personal communication) are currently preparing a review on this subject.

The dynamics of enzymatic digestive processes, also in view of compartmentation and different ways of activation of zymogens, and a seasonal analysis of membrane-bound digestive enzymes of the midgut gland were presented by R. Saborowski at this conference (and as a personal communication). Some aspects of digestive enzyme regulation in *M. norvegica* are discussed in conjunction with more numerous results on *E. superba* in the present paper (see next section). The stomach of *M. norvegica* also contains bacteria that produce digestive enzymes. However, the potential contribution of these enzymes to krill digestion appear negligible in relation to endogenous enzyme production in the krill midgut gland and stomach (Donachie et al. 1995).

Euphausia superba, strictly polar: adaptations in respiration and enzymes

Respiration

A multitude of data already exist on respiration rates in *E. superba*. Rates were mostly determined to establish length or weight relationships in order to assess energy requirements in krill. They were used furthermore to establish energy budgets to assess the krill's capacity to adjust to seasonal variation. Moreover, thermal adjustments are discussed.

Recently, direct winter–summer comparisons of respiration rates were also conducted with respect to seasonal adjustments, particularly in view of the unsolved riddle of how krill cope physiologically with the long winter in the Antarctic. Kawaguchi et al. (1986) were the first to report, and Quetin and Ross (1991) and Torres et al. (1994) presented data that showed metabolic reductions during winter as compared with summer values. These reductions were about 33 and 45%, respectively. Such metabolic reduction was interpreted as a way to reduce physiological activity generally in order to adjust to diminished food levels during winter. This refers to primary production in the open sea as well as that in under-ice algae, which krill are known to utilize (e.g., Marschall 1988). Since information on the feeding habits, including a possible switch to carnivory (Atkinson and Snyder 1997), is still incomplete, much debate was generated (e.g., Huntley et al. 1994).

A summary of respiratory data is published in Opalinski (1991). From available tables, a graph was constructed to give an overview of the respiratory dependence on size (weight) and temperature (Fig 6*a*).

From Fig. 6*a*, it is obvious that respiration is dependent on both body size (weight) and experimental temperatures. However, a large range of data scatter prevails. For this reason, a more thorough analysis was not attempted here, e.g., to calculate mathematical relationships. Nevertheless, a trend is visible in which both size and temperature typically follow exponential curves (Quetin et al. 1994; Torres et al. 1994). However, there is a general problem in obtaining reliable data in a pelagic (planktonic) organism under necessarily confined conditions in a measuring chamber.

In terms of temperature adaptation, comparisons within congeneric species from different latitudes have been useful (Hochachka and Somero 1984). Size apparently matters as well. Although not congeneric, *M. norvegica* is a large euphausiid and may thus be comparable to *E. superba*. Accordingly, respiration data for *E. superba* taken from the above data set were integrated into Fig. 6*b* in a comparable size range of 20–100 mg dry weight and were contrasted with the complete data set on *M. norvegica* from the Ligurian Sea, Clyde Sea, and Kattegat (standard size 50 mg dry weight).

The exponential curves for *M. norvegica* appear to link with the single data points for *E. superba* in the low temperature range. The spread of data in the former indicates the range of respiratory adaptation across geographic regions. An equal adaptive potential appears to relate to Antarctic krill from different areas of the polar ocean within its narrow range of temperatures (–2 to 2°C). However, metabolic cold compensation (sensu Hochachka and Somero 1984) does not seem to be pronounced in *E. superba* because a shift to

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higher respiratory levels at low temperatures would have been expected in the interspecies comparison in view of the strong latitudinal thermal contrast (–2 to 16°C).

At any rate, future more thorough comparisons of the two euphausiid species appear feasible using standardized equipment. A prerequisite to following these lines would be to further optimize respiration chambers and to take utmost care in reproducing the same measuring conditions in seasonal or systematic comparisons. The same applies to intraspecific comparisons of respiration rates in relation to seasonal, particularly nutritional, adaptations.

Metabolic enzymes: CS

As in *M. norvegica*, adjustments of the basic characteristics temperature maximum and thermal stability in CS are unimportant in temperature acclimatization in *E. superba*. A substantial reduction in the energy of activation may play a role (Vetter 1995*a*), which was partly confirmed in our laboratory but is apparently influenced by individual and (or) geographic variation (R. Müller, Alfred Wegener Institut for Polar and Marine Research, c/o Biologische Anstalt Helgoland, Marine Station, Postfach 180, D-27483 Helgoland, Germany, personal communication). Experimental acclimation showed no capacity to adjust specific activities to varied temperatures (Vetter 1995*a*). All of these results underline the strictly stenothermal characteristics in the Antarctic krill.

In a north–south comparison of enzymatic regulation in different crustaceans, it appeared that one way to compensate for the rate-limiting, constantly cold environment in the Antarctic is maintaining higher enzyme concentration. Concerning CS, the polar euphausiid produces about five times the amount of CS protein as *M. norvegica* (by way of immunodetermination and ELISA; R. Müller, Alfred Wegener Institut for Polar and Marine Research, c/o Biologische Anstalt Helgoland, Marine Station, Postfach 180, D-27483 Helgoland, Germany, personal communication).

A previous comparison of northern and Antarctic krill revealed a mechanism to enhance enzyme regulation (Vetter 1995*b*). The compared euphausiids showed generally low levels of enzyme inhibition (K_i), such an effect being the prerequisite for high regulatory capacity. ATP controls CS activity via feedback inhibition. At low ATP levels, the enzyme is activated. With increasing citrate production, more ATP is produced in the end, and the resulting higher levels of ATP then inhibit the turnover of the substrate acetyl-CoA. This alternating activation–inhibition mechanism is possibly unique to euphausiids and apparently is coupled to the specific strictly pelagic way of life, requiring constant swimming. A high capacity for control helps in optimizing CS activity in relation to the high and fluctuating energy demand in euphausiids.

What becomes clear is that CS activity and respiration rates do not appear to be strongly related, particularly in the case of northern krill in the Ligurian Sea. This corresponds to findings for other invertebrates (Thuesen et al. 1998). Generally, further studies on actual substrate concentrations, the control function of metabolites, and the feedback mechanisms that modulate enzyme activity appear to be a promising field in euphausiid ecophysiology.

Digestive enzymes

The structural components of chitin are amino sugars. However, chitin is one of the most resistant and hardy substances in nature. The ability to use or reuse chitin, i.e., to break it down enzymatically into the sugar components, would mean a considerable gain of energy for any organism.

Chitin-degrading enzymes are widely found in most animal taxa (Jeuniaux 1966) but have rarely been identified in marine zooplankton (Buchholz 1993). In krill, two main sources of chitin are available. Firstly, several *Thalassiosira* species contain large amounts of chitin and are very common in the Atlantic, and particularly in Antarctic waters. The species is a staple food of krill (see Saborowski and Buchholz 1999). Secondly, copepods and other small crustaceans with chitinous exoskeletons are major food items of *M. norvegica*. However, this also appears to be the case for *E. superba*, at least during the southern winter (e.g., Pakhomov et al. 1997). Accordingly, we attempted to identify in krill the enzymes necessary to cleave chitin and compare activities and the dynamics of digestive enzyme induction.

The chitin-degrading enzymes in krill consist of an endochitinase that produces oligomers and three isoforms of an exochitinase that liberate the amino sugars (Spindler and Buchholz 1988). This set of enzymes has a double function. Firstly, they show high activity associated with the moult cycle and are responsible for reabsorption of the old cuticle prior to ecdysis. It is interesting to note that the capacity for the moult-related turnover of chitin corresponds to that of tropical insects (Buchholz 1989; Buchholz and Buchholz 1989) and thus highlights the physiological performance in the Antarctic krill. Secondly, they function as true digestive enzymes and occur at high activities (Buchholz and Saborowski 1996; Saborowski and Buchholz 1999) in the midgut gland and stomach in krill. Using immunotechniques, the functions of the exochitinase (*N*-acetyl-β-D-glucosaminidase (NAGase)) were further differentiated.

While one enzyme, NAGase B, plays a significant role in the animal's moult cycle, the other one, NAGase C, participates in the digestion of a chitin-containing diet. NAGase B followed a moult cycle related pattern of activity and was almost exclusively localized in the integument (Fig. 7*a*). The activity of NAGase C was independent of the moult stage of the animal and was predominantly found in the gastrointestinal tract (Fig. 7*b*) (Peters et al. 1998 and 1999).

The diet-induced form shows high variability in activity, reflecting most probably different nutritional states of the specimens taken from the field due to induction of NAGase synthesis by an appropriate chitinous diet. Furthermore, the lack of moult-related activity indicates that food ingestion and digestive processes are not reduced around ecdysis, such as in other crustaceans (see Buchholz 1989). The high energy demand in krill may prohibit periods of extended fasting around moult, forcing these animals to immediately resume feeding after moult. This effect may be further facilitated by the extremely rapid ecdysis, which takes no more than a few seconds (Buchholz 1991).

In a seasonal analysis, chitinolytic activity was compared with alkaline protease in the midgut gland and stomach in *E.superba* (Buchholz 1989). The digestive chitinases and the protease were similarly active during austral summer and

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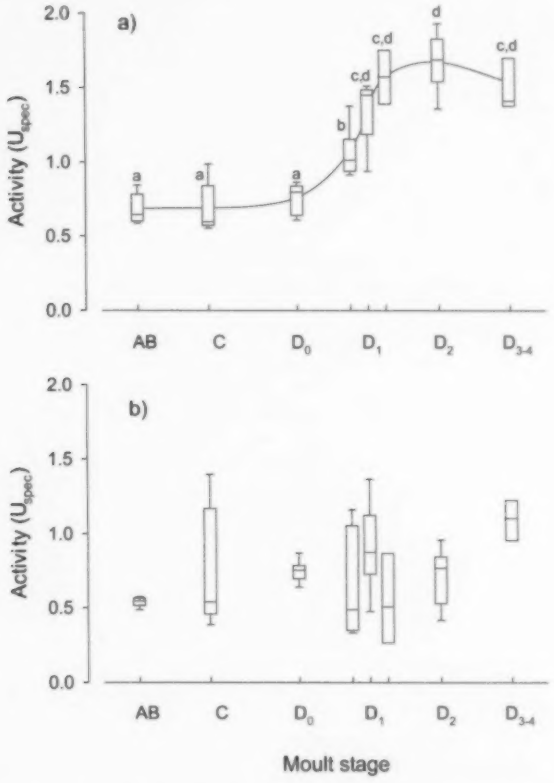
Fig. 7. Specific activities of the exochitinase (*a*) NAGase B (from integument extracts) and (*b*) NAGase C (from stomach extracts) in specimens of *E. superba* of different moult stages determined by immunotitration using a specific polyclonal antibody (n = 4–8). Values with the same letter in (*a*) are nonsignificant differences (ANOVA and Student–Newman–Keuls test, $p > 0.05$). Source: Peters et al. (1999).

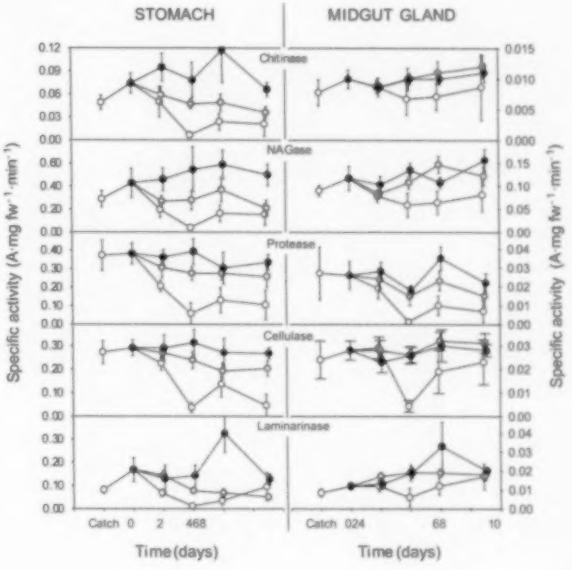


winter (August, September). This may indicate that feeding levels were maintained at a comparable level throughout the year. As phytoplankton levels were low during winter in the area of sampling (South Georgia; Priddle et al. 1990), a switch to zooplankton ingestion and associated induction of chitinases could not be excluded. A more thorough analysis in that respect is intended in the near future.

Activity levels in *M. norvegica* displayed generally considerably higher values with higher variation than in *E.superba*, probably as a consequence of the omnivorous behaviour in the northern krill species, the variability depending on the recently ingested food type. Chitinolytic activity was also analysed in the integument in *E. superba*: similar levels of activity indicate maintenance of reabsorption of cuticle chitin and thus the continuation of moulting processes during overwintering.

With the aim of testing the capacity of krill to cope with an unpredictable food supply in the Antarctic, a laboratory study of the induction of a set of digestive enzymes, including chitinases, in response to different feeding conditions was conducted (Saborowski and Buchholz 1999). Krill were either starved or fed with the diatom *Dunaliella* or alternatively with *Cyclotella*, which contains chitin at 12% of its dry weight.

Fig. 8. Time courses of specific activities of digestive enzymes in the stomach and midgut gland of krill maintained in a feeding experiment for 9 days. Solid circles, fed with chitinous *Cyclotella*; grey circles, fed with nonchitinous *Dunaliella*; open circles, starved (n = 4–15). Source: Saborowski and Buchholz (1999).



Characteristic time courses of the activities in exo- and endo-chitinase, protease, laminarinase, and cellulase were evident after 4 days. In specimens fed with *Cyclotella*, rich in both chitin and laminarin, chitinase and laminarinase were coinduced above the initial value. In starved animals, in contrast, enzyme activities in the stomach decreased to a minimum after 4 days but recovered within 14 days to the values at the start of the experiment (Fig. 8; 14- and 20-day experiments not shown). Specific activities of all enzymes were affected less by feeding regime in the midgut gland than in the stomach but otherwise followed a similar pattern.

The initial decrease in activity in the stomach during starvation can be explained by diminished secretion of enzymes from the midgut gland into the stomach (Saborowski and Buchholz 1999). At the same time, persistent activities in the midgut gland provide a digestive potential that can immediately be used when a rich food patch is encountered by Antarctic krill. The ability to maintain high levels of activities in a whole set of enzymes and additionally to enhance specific enzymes with an increase in a particular substrate can be considered an efficient adaptation to the variable Antarctic trophic environment, which requires rapid and effective nutrient utilization.

The enigma of DVM, and metabolic adaptation in *M. norvegica*

The impressive performance in DVM has long been known in *M. norvegica* (Mauchline 1960). In *E. superba*,

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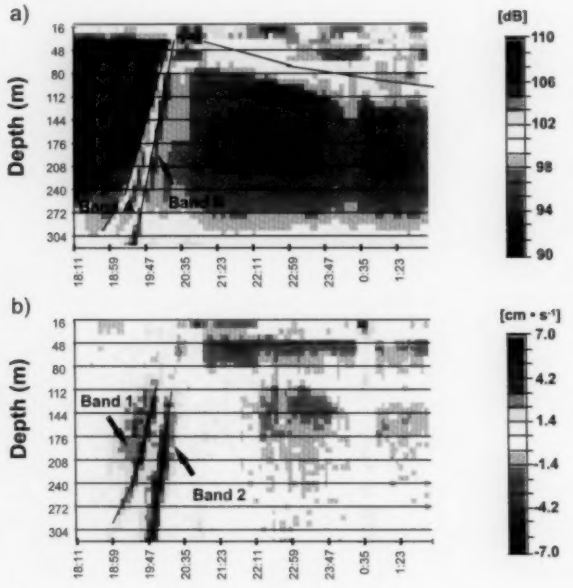
Fig. 9. Real-time ADCP recordings of DVM in zooplankton in the Ligurian Sea. (*a*) Backscatter at 150 kHz; (*b*) vertical velocities. Band B and band 2 relate to *M. norvegica*. Source: PEP database and G.A. Tarling (personal communication). Method in Tarling et al. (1999*a*).



analogous behaviour is much less expressed (Klusek and Godlewska 1988).

In a recent study of *M. norvegica*, behavioural investigations using sonar and multinet equipment (Tarling et al.1998*a*, 1999*a*; Guérin-Ancey et al.1998) were able to be combined with data on energy requirements. A short summary of DVM behaviour is given below as a background to considerations of energy metabolism in *M. norvegica*.

The largest amplitude of DVM is typical of *M. norvegica* in the Mediterranean (Fig. 9). Over depths of more than 2000 m, krill migrate in spring some 800 m daily, whereas 500–600 m appears to be the summer amplitude (Velsch 1997).

In very elegant experiments, Velsch and Champalbert (1994) and Velsch (1997) demonstrated a clear influence of an underlying endogenous control. Here, the natural light cycle of the sun is the zeitgeber. However, the moon is also influential and appears to phase "midnight sinking", i.e., after "dipping" for a short time into the warm top layers, krill sink near midnight to depths of about 100 m before the sunrise induces the rapid morning descent (Tarling et al. 1999*a*).

In the Clyde Sea and Kattegat, the range of DVM is restricted by shallower depths of 150 and 130 m, respectively. Nevertheless, regular DVM prevails during summer and winter, closely following the solar light cycle, apparently setting the clock of an endogenous rhythm. However, the cyclical behaviour is modified to a large extent by external and internal cues.

Firstly, only a certain proportion of the krill seems to migrate at all (Fig. 10). This was assessed at two-thirds of the population in the Clyde Sea and at one third in the Kattegat (Tarling et al. 1998*a*). Secondly, at both locations, krill not only feed during nighttime in the upper layers but also during daytime in the deep (Buchholz et al. 1995; Lass et al. 2000). Apparently, there is only a limited need for DVM in terms of trophic cues. Furthermore, a tendency for smaller krill to migrate at a larger amplitude than larger krill was confirmed (Mauchline 1960), probably dependent on the considerable increase in energetic requirements with weight (Tarling et al. 1998*a*; Saborowski et al. 2000*b*).

Energetic requirements increase drastically with temperature. The relative carbon demand was calculated from temperature-dependent respiration at the Kattegat location (Fig. 11).

If krill, for example, migrate from the deep layers at 6°C to above 50 m where the temperature increases to 12°C during summer, a 50% increase in carbon demand ensues. There seems to be a trade-off between the favourable enhancement of motility due to the temperature increase and the high energy expenditure in the upper warm layers. Krill may suspend DVM for one or more diel cycles before crossing the thermocline again (Saborowski et al. 2000*b*).

An intensive study of DVM in the Kattegat was conducted over 10 days during summer 1998 (Tarling et al. 1999*b*). It was shown that internal cues, depending on the moult and reproductive cycles, can modify DVM behaviour and the range of DVM.

In both female krill (Fig. 12) and male krill (data not shown), an intensive phase of moulting was encountered during the summer study. Obviously, krill moulted only at depth and predominantly during nighttime. In this way, having a soft exoskeleton for about 2 days, krill can "hide" in the dark deep and thus avoid predation and (or) cannibalism during this phase of vulnerability. Moreover, due to the energy-intensive processes of shedding the old shell and hardening the new one, krill suspend DVM during this time.

In contrast, female krill that were ready to spawn (identifiable by the blue–grey tint of the ovary; Cuzin-Roudy and Buchholz 1999) were almost exclusively found in the warm upper layers of the Kattegat. By crossing the thermocline, the physiological advantage would be an acceleration of the final stages of egg maturation and of the spawning process itself. Furthermore, spawned eggs and the first larval stages would be positioned in favourable surroundings, i.e., warm and plankton rich.

In summary, krill seem to be generally better adapted to the deeper and cooler water layers at all three sites. DVM apparently is controlled endogenously, but krill are able to adapt the range of migration (and possibly the frequency of DVM) to physiological necessity to a large extent. To modify internal rhythms more or less continuously depending on a multitude of external and internal cues requires a high level of physiological plasticity, which appears to be typical for *M. norvegica*.

At any rate, energetic requirements and DVM are intimately interlinked. A practical way to differentiate and better understand the complex interdependencies would be to use a modelling approach. A first attempt to integrate physiology and behaviour in *M. norvegica* was presented by G.A. Tarling et al. (Scottish Association for Marine Science, P.O. Box 3, Oban, Argyll PA34 4AD, U.K., personal communication) during this conference in the form of an optimal-foraging model. Here, another important influencing factor

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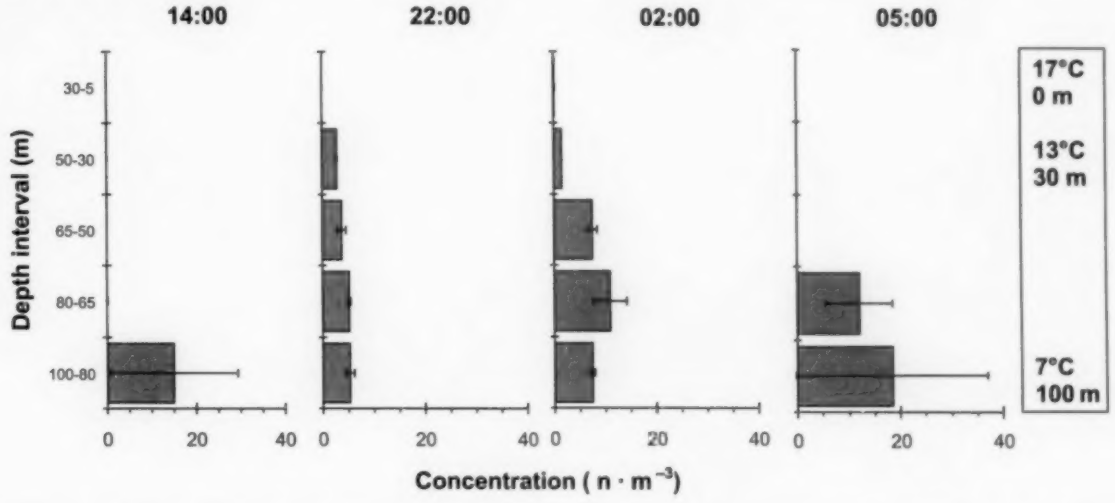
Fig. 10. Concentration of *M. norvegica* in the Alkor Deep, Kattegat, averaged over seven day–night cycles within the period 24 July – 3 August 1998 (with 95% confidence intervals). The pattern shows a vertical migration into the upper layers during nighttime from a daytime location in the deep.



in DVM can also be addressed and integrated: predation pressure.

Seasonality in euphausiid physiology

In the following, the adaptive features described above are summarized in view of seasonal adjustments of rates of respiration and metabolic and digestive enzymes in both krill species.

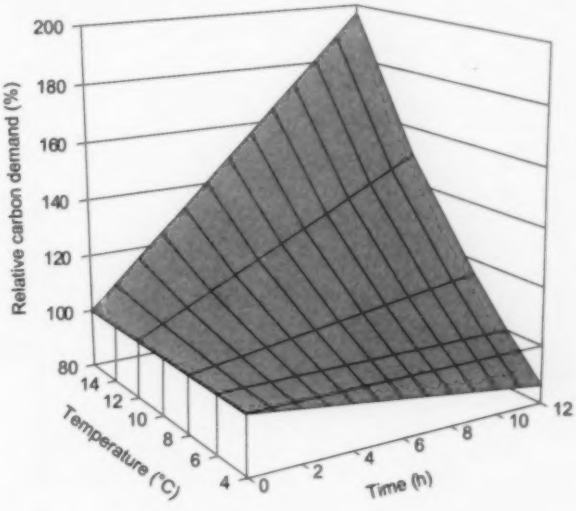
Meganyctiphanes norvegica

Apparently, no real food shortage exists during the seasons in the Clyde Sea and Kattegat. Nevertheless, a drastic winter reduction occurs in both ambient Chl *a* levels and food ingested in the Clyde Sea krill (Table 2). In the Kattegat, in contrast, continuous advection supplies copepods, the staple food of krill at that location, during summer as well as winter. As a consequence, no seasonal respiratory adaptation is noted. However, the vertical shift of the respiration curves suggests an overall adaptation to the different thermal regimes at the two sites.

The case of the Ligurian Sea is different from both of the northern sites: *M. norvegica* has to cope with an oligotrophic situation during most of the year. Accordingly, a strong metabolic enhancement coupled in time to the short winter–spring plankton blooms occurs to maximize growth and reproduction. However, the summer–fall curve of respiration is at a similar level as in the north, although shifted parallel so that a similar level of 30–35 μmol O_2·mg dry weight^{-1}·h^{-1} is maintained at all three sites. This respiratory value may be seen as a common basal metabolic level to maintain physiological functions.

Similarly, in CS, a basal level of K_m values prevails in krill at all three sites during winter. At the northern locations, a summer maximization of substrate affinity is notable, apparently linked to the development of the temperature differential of the water columns. This adaptation may be seen as an indication that krill in fact make use of temperature-linked enhancements of physiological functions, e.g., with respect to motility and reproductive processes.

Fig. 11. Relative carbon demand as related to oxygen consumption versus environmental temperature and time spent at these temperatures in *M. norvegica* at the Kattegat location. Source: R. Saborowski (unpublished data) and Saborowski et al. (2000*b*).



Here, the Ligurian krill is completely different again: the drastic increase in substrate affinity during the oligotrophic summer–fall phase may compensate for the somatic reduction expressed as the decrease in specific activity of muscle CS. In short, the Mediterranean krill appear to be more influenced by the seasonal trophic regime than krill at the northern sites, where temperature effects are more important. The differences found in respiratory and metabolic enzy-

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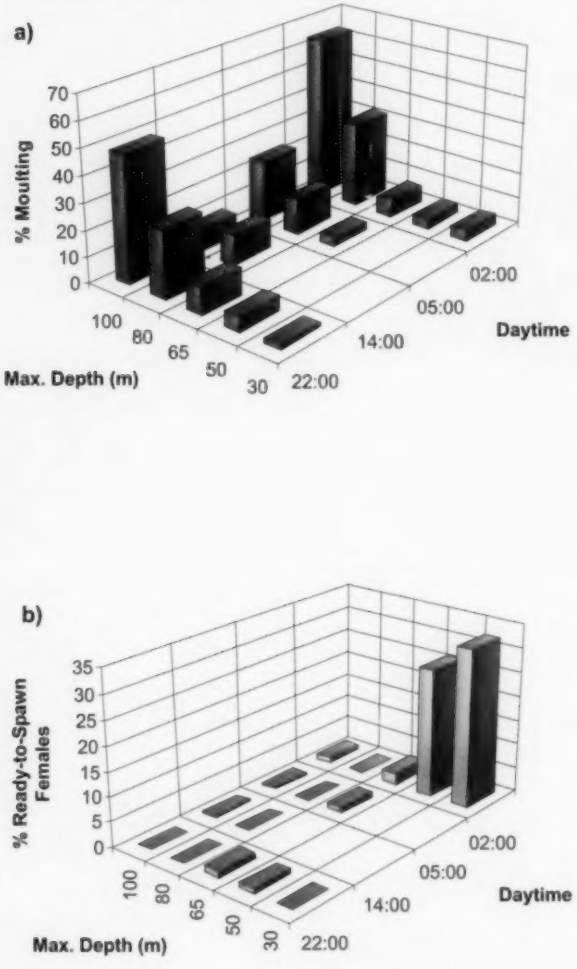
Fig. 12. (*a*) Percentage of moulting *M. norvegica* versus diel depth distribution (females) and (*b*) percentage of ready-to-spawn female *M. norvegica* versus diel depth distribution (the ovary of ready-to-spawn krill attains a blue–grey tint and can be easily spotted in fresh samples). Averaged from data obtained from MOCNESS nets deployed over seven full day–night cycles between 24 July and 3 August 1998. Source: F. Buchholz (unpublished data). Methods in Tarling et al. (1999*b*).



matic adaptation may be reflected in the clear genetic separation of the Ligurian population from all Northeast Atlantic ones (Zane and Patarnello 2000; Zane et al. 2000).

Meganyctiphanes norvegica is a strong feeding opportunist and alternates between phyto- and zoo-plankton, making use of a wide variety of species. The inducability of digestive enzymes including chitinases is perfectly tuned to this physiological flexibility. Furthermore, egg production and the length of the reproductive period are both controlled by the specific temperature regime and trophic conditions at the three sites (Cuzin-Roudy and Buchholz 1999; and Cuzin-Roudy 2000). Moreover, krill are able to modify DVM behaviour according to physiological necessity with respect to moult, reproduction, and overall energetics.

In conclusion, *M. norvegica* is characterized by a high level of physiological plasticity, which may be the prerequisite for the evolutional success of the species. This is reflected in its exceptionally wide distribution.

Euphausia superba

For *E. superba*, tendencies towards metabolic reduction as an overwintering strategy have been reported (Quetin et al. 1994; Torres et al. 1994). If a latitudinal comparison may be allowed, a different strategy in *M. norvegica* would appear: the northern krill maintains a comparable oxygen consumption at all three sites during winter but shows enhanced metabolism during the productive spring phase in the Mediterranean with respect to a common basal metabolic level.

However, the enzymatic repertoire of *E. superba* shows an equal potential for physiological plasticity as in *M. norvegica*. The Antarctic krill may use variable food sources wherever it finds them, i.e., phyto- and zoo-plankton as well as under-ice algae. Furthermore, the growth parameters are kept equally flexible (Buchholz 1991): krill may even shrink as a last resort to compensate for diminishing energy reserves during winter (Nicol et al. 1992).

It may be considered a less important question whether krill reduce or enhance metabolic rates. Nevertheless, krill are apparently able to make use of any improvement in environmental conditions and to transfer these immediately into maintenance of vital functions irrespective of season and as far as possible into those of growth and reproductive processes.

Perspectives

A worldwide comparison of temperate euphausiids may be envisaged in the near future: in particular, knowledge on *M. norvegica*, *Euphausia pacifica*, and *Thysanoessa* spp. is emerging rapidly. To elucidate patterns of DVM and the underlying physiology may serve as a unifying approach. In this case, a combination of methods can be applied: at the population level, ADCP and multifrequency sonar, groundtruthed by multinet catches, may be employed. In linked physiological studies, modern energy budgets should be constructed with parameterization appropriately tuned to modelling. Progress has been achieved in combining physiological models, e.g., optimal-foraging models, and physical (advection) models. Several examples of such approaches appear to be underway, e.g., *E. pacifica* is a target species of Northeastern Pacific GLOBEC (Global Ocean Ecosystem Dynamics) and *M. norvegica* is planned to be studied in the Arctic and Northeast Atlantic fjords, which may serve as "model oceans." A coordination of initiatives would be desirable. A transfer of methodology and results with respect to Antarctic krill appears to be sensible.

Further adaptational and life history data are needed to complement population assessments in *E. superba* in view of currently growing plans for krill utilization. To use standardized equipment, e.g., appropriate devices for respiration measurements, for consistent seasonal, latitudinal, and interspecies comparisons, appears to be a necessity. State-of-the-art methodology for studies of population genetics is available and may serve to highlight functional biodiversity,

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as exemplified here for *M. norvegica* as well as large-scale gene flow. Biochemical features may be usable as spinoffs: digestive enzymes in krill may be characterized and then used in pharmaceutical technology.

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Krill (Euphausiacea) life history and aspects of population dynamics

Volker Siegel

Abstract: The present perspective summarizes information on the variability of krill population parameters, which can assist in interpreting fluctuations in euphausiid populations. This requires knowledge about potential longevity of an individual as well as the age composition of populations. Further key parameters of the life cycle are discussed for a number of euphausiid species from oceans around the world. In a variable environment, species may show variations in sex ratio, breeding season, larval development, as well as functional characteristics such as natural mortality and productivity. Conceptual models based on results for some krill species indicate that environmental disturbances create instability in populations by reducing the recruitment success, which finally can lead to a decreasing population size.

Résumé : La présente synthèse résume l'information sur la variabilité des paramètres des populations de krill, ce qui peut aider à interpréter les fluctuations dans les populations d'euphausiacés. Il faut pour cela avoir des connaissances sur la longévité potentielle d'un individu ainsi que sur la composition par âge des populations. Nous analysons d'autres paramètres clés du cycle vital pour un certain nombre d'espèces d'euphausiacés présentes dans divers océans du monde. Dans un environnement variable, les espèces peuvent présenter des variations dans le rapport des sexes, la saison de reproduction, le développement larvaire ainsi que dans des caractéristiques fonctionnelles comme la mortalité naturelle et la productivité. Les modèles conceptuels basés sur les résultats concernant certaines espèces de krill indiquent que les perturbations de l'environnement créent de l'instabilité dans les populations en réduisant le succès de recrutement, ce qui peut aboutir à une diminution de la taille des populations.

[Traduit par la Rédaction]

Introduction

In many euphausiid species, life cycle evolution has involved adaptation to long winters with low temperatures and poor nutritional conditions interspersed with seasons of high productivity prompted by seasonal upwelling events. These scenarios must have occurred over evolutionary time in sufficiently predictable patterns to allow krill to adapt and possibly fill key positions in marine ecosystems worldwide. In the present-day scenario, where long-term climate changes seem probable, questions arise if and possibly how krill population dynamics will be affected by such changes. More explicitly, what potential effect do regional climatic changes have on stock structures, life cycle, and survival rates of euphausiid species? Furthermore, what impact will such changes in krill stocks have on dependent higher trophic levels in marine ecosystems?

Against this background, factual knowledge about basic krill population parameters such as growth, reproduction, and recruitment productivity and their variability under "normal" conditions seems to be essential to identify and quantify potential changes. Different species will certainly react differently due to their own plasticity in their life cycle, even in this morphological homogeneous group. Based on complex field data, hypotheses have been developed that might help to improve models of krill distribution and abundance and population processes. This may finally help to converge the theoretical view and the natural world.

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Life history

Populations are not composed of a series of identical individuals. Two major variables distinguish individuals in populations: sex and age. Since it is only the females that reproduce, the ratio of females to males is a matter of significance and will clearly affect the potential reproductive rate of the population. Age is a significant variable for krill populations because older individuals are larger and size differences affect maturity and fecundity. Once we obtain estimates of abundance, we can investigate primary demographic parameters such as mortality and productivity.

Sex ratio

Over several years (1985–1989) in the Barents Sea, the sex ratio of *Thysanoessa inermis* was fairly constant and close to equal numbers for males and females (Dalpadado and Skjoldal 1991). The same ratio of 1:1 was observed for *T. inermis* and *Thysanoessa raschii* off northern Norway (Falk-Petersen and Hopkins 1981). Tanasichuk (1998*a*) determined a sex ratio of 1:1 for *Thysanoessa spinifera* in waters of British Columbia and could not detect any significant changes over 6 years. The same grand mean was perceived for *Euphausia pacifica* off British Columbia. The species just showed random fluctuations within and between years but no significant deviation from the average situation (Tanasichuk 1998*b*). However, off California, sex ratios for *E. pacifica* ranged from 1:1 to 3:1 in favour of females. Possible reasons for this high portion of females can be misidentification, net

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avoidance of larger males, higher mortality of larger males, different growth rates between sexes, with a slower growth rate for females, and possibly a shorter life span for males using more energy for fast growth (Brinton 1976). In samples taken during a large-scale survey across the entire Scotia Sea, male and female *Thysanoessa macrura* made up 37% each (ratio 1:1). The sex ratio for the Antarctic krill *Euphausia superba* varies randomly over single seasons and interannually, respectively. The long-term average proportion is 0.52, and thus, the composition of the population hardly deviates from the expected 50% sex ratio (V. Siegel, unpublished data).

The early production of spermatophores by male krill, the continuous production of ripe spermatophores in males during the spawning season, and the presence of additional spermatophores in the male ducti help the replacement of spermatophores that were attached to the females thelycum and are shed and lost with every new moulting cycle. This behaviour allows the euphausiids an equal number of males; otherwise, the sex ratio would have to favour the proportion of males in the spawning stock to allow a successful fertilization of the breeding females. In this regard, it is difficult to explain why male *E. superba* attain sexual maturity 1 year later than females (Siegel and Loeb 1994) and still represent an equal sex ratio if they are not highly efficient in producing spermatophores.

Reproduction

Timing in spawning seasons varies among species and within species. Spawning seasons may occur year-round where seasonal cycles are weak or be restricted to a brief period during the annual seasonal cycle with cold, low light, and low food availability during winter periods. However, some species just prefer these harsh winter conditions to commence spawning (e.g., *T. macrura*), whereas others at the same geographical latitude wait for summer conditions and for whatever factor might be of advantage to them during this time of the year.

The year-round occurrence of gravid females of *Euphausia hanseni* in the Benguela upwelling system indicates that the species breeds continuously (Barange and Stuart 1991). However, it is uncertain whether sampling density was really dense enough to distinguish between multiple spawning (four to six times a year) like in *E. pacifica* off California and continuous breeding. *Euphausia lucens* in the Benguela upwelling region is also thought to display continuous spawning (Pillar and Stuart 1988). There is variation in the quality of spawning during the season. Mostly large females produce a large amount of eggs in early spring (August–September), while smaller females spawn fewer eggs mainly during summer (November–January) and winter (May–July).

The major *E. lucens* spawning event takes place just prior to the onset of upwelling causing the spring phytoplankton bloom. In the case of this omnivorous species, the subsequent development of the zooplankton stock may be of additional importance. On the other hand, temperature and salinity are not thought to be important factors controlling the breeding cycle. On the contrary, gravid females of *E. lucens* show a large tolerance to these environmental parameters. This coincides with the observations on *E. pacifica*, which reaches highest densities and spawning intensities during upwelling because the proximate cause for this behaviour is food availability, i.e., phytoplankton concentrations with latitudinal changes in timing (Smiles and Pearcy 1971; Brinton 1976; Ross et al. 1982). Off Tasmania, *Nyctiphanes australis* attains highest abundance in summer, but spawning intensity again seems to be related to optimum food supply (Ritz and Hosie 1982).

Seasonal breeding is common in temperate and polar species, but at the same time, interannual variation in timing of spawning can be found. A good example is the breeding season of *Meganyctiphanes norvegica*, which varies with latitude. In the Mediterranean, females are reproductively active during winter (January–April), in the English Channel, they do not start before February, and off Scotland and southern Norway and in the Gulf of St. Lawrence, spawning takes place in summer (May–July). This variation in spawning behaviour led to the suggestion that reproductively isolated populations may exist. Despite the latitudinal differences in timing and duration of the reproductive season, the pattern of ovarian development is identical for the different areas. However, spawning periods may vary interannually in length and timing; the onset and completion of the reproductive period can change by approximately ±1 month over the distribution range (Cuzin-Roudy and Buchholz 1999).

In the southern Bering Sea, *T. inermis* spawning generally starts on outer shelf areas, while it is delayed to mid-April on the middle shelf. Spawning of *T. raschii* is even later; it does not start before mid-May on the shelf (Smith 1991), but this author already pointed out that warmer conditions in some years did not induce earlier spawning for *Thysanoessa* species but led to larger sizes of the animals, which she attributed to higher growth rates. This is interesting because another euphausiid species, *E. pacifica*, shows a plasticity in life history pattern over its distribution range, especially geographical differences in breeding seasons (Iguchi et al. 1993; Iguchi and Ikeda 1995), e.g., off Japan in February–May, off Kamchatka in May–June, in the Sea of Okhotsk in June, off Oregon in September, and year-round in coastal British Columbia and California. Most authors related this to the onset of the highly productive upwelling season. This may also explain why Tanasichuk (1998*b*) found no obvious changes in spawning patterns between pre-ENSO (El Niño Southern Oscillation) years and the warm El Niño periods. Possibly, productivity was still high enough to support a regular reproduction process.

Thysanoessa raschii and *T. inermis* are spring breeders in northern Norwegian waters. The exact breeding seasons of the two species deviate slightly from one another. Accompanying the temperature change in the Barents Sea system and the shift in distribution patterns, the *Thysanoessa* stocks were thought to show a response to later spawning during the cold periods. During warm years, spawning ended in May–June, while it was prolonged in cold years and did not end before July–August, which had, of course, effects on the capelin and juvenile cod (feeding on prespawning euphausiids) and adult cod stocks (feeding on postspawning krill concentrations) in the region (Drobysheva 1994).

However, temperature may not be the direct cause for a biological response of the Barents Sea euphausiids. Evidence

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Table 1. Longevity, age at maturity, and age at first spawning for euphausiid species.

Species	Geographic region	Maximum age	Age at maturity	Age at first spawning	Reference
T. raschii	Southern Norway	1+	1+	1+	Lindley 1980
T. raschii	Boreal	2+	1+	1+	Einarsson 1945
T. raschii	Subarctic	2+	2+	2+	Einarsson 1945
T. raschii	Arctic	2+	2+	No spawning	Einarsson 1945
T. raschii	Southern Barents Sea	2+	1+	2+	Drobysheva 1987
T. raschii	Northern Norway	2 years 3 months		Few 1+ F, few 1+ M	Falk-Petersen and Hopkins 1981
T. raschii	Eastern Greenland	3+	2+	2+	Lindley 1980
T. inermis	Southern Norway	1+	1+	1+	Lindley 1980
T. inermis	Boreal	2+	1+	1+	Einarsson 1945
T. inermis	Subarctic	2+	2+	2+	Einarsson 1945
T. inermis	Arctic	2+	2+	No spawning	Einarsson 1945
T. inermis	Southern Barents Sea	2+	1+	2+	Drobysheva 1987
T. inermis	Northern Iceland	2+	1+ M, 2+ F	1+ M, 2+ F	Astthorsson and Gislason 1997
T. inermis	Northern Norway	2 years 3 months		Few 1+ F, most 1+ M	Falk-Petersen and Hopkins 1981
T. inermis	Barents Sea	3+	2+	2+	Dalpadado and Skjoldal 1995
T. inermis	Greenland	3+	3+	3+	Lindley 1980
T. inermis	Pacific, Northeastern Aleutians	3+	3+?	3+?	Nemoto 1957
T. inermis	Pacific, Southeastern Aleutians	2+	2+	2+	Nemoto 1957
T. longicaudata	North Atlantic, oceanic	2+	1+	1+	Einarsson 1945
T. longicaudata	Northern Iceland	1+	1+	1+	Astthorsson and Gislason 1997
T. acutifrons	North Atlantic, deep water	2+	2+	2+	Einarsson 1945
M. norvegica	Mediterranean	1+	1+	1+	Lindley 1982*a*
M. norvegica	Scotland	2+	1+	1+	Mauchline and Fischer 1969
M. norvegica	Skagerrak	2+	1+	1+	Einarsson 1945
M. norvegica	Skagerrak	2+	1	1+	Boysen and Buchholz 1984
M. norvegica	Northern Iceland	2+			Astthorson and Gislason 1997
M. norvegica	Western Norway	2+			Lindley 1980
M. norvegica	Northern Norway	2 years 6 months		No spawning	Falk-Petersen and Hopkins 1981
E. pacifica	Oregon	1 year	1 year	1 year	Smiles and Pearcy 1971
E. pacifica	Southern California	6–8 months, spring R	4 months	4 months	Brinton 1976
E. pacifica	Southern California	10–13 months, fall R	7 months	7 months	Brinton 1976
E. pacifica	Northeastern Japan	15 months			Iguchi et al. 1993
E. pacifica	British Columbia, Canada	19–22 months			Nicol and Endo 1997
E. pacifica	Northwest Pacific	2+	1+	1+	Ponomareva 1963
E. pacifica	Northwest Pacific	2+	1+		Nemoto 1957
E. pacifica	North Pacific, Aleutians	2+			Iguchi and Ikeda 1995
E. pacifica	Northern Japan	2+ F, 1+ M	1+	1+	cf. Nicol and Endo 1997
E. pacifica	Southwestern Japan	21 months			Iguchi et al. 1993
N. capensis	Benguela Current	6 months			Barange and Stuart 1991
E. hanseni	Benguela Current	6 months			Barange and Stuart 1991
E. lucens	Benguela Current	10 months	6 months		Stuart and Pillar 1988
T. spinifera	British Columbia, Canada	10 months			Tanasichuk 1998*a*
N. australis	Tasmania		3.5–4 months	3.5–4 months	Hosie and Ritz 1983
N. simplex	Baja California, Mexico	9 months	63 days	63 days	Gomez 1995
N. simplex	Baja California, Mexico	7–8 months	30 days		Lavaniegos 1995
E. eximia	Baja California, Mexico	326 days	215 days	215 days	Gomez 1995
E. frigida	Antarctic Peninsula	1+	1+	1+	Siegel 1987
E. triacantha	Antarctic Peninsula	2+	1+	1+	Siegel 1987

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Table 1 (*concluded*).

Species	Geographic region	Maximum age	Age at maturity	Age at first spawning	Reference
E. crystallorophias	Antarctic Peninsula	4+	2+	2+	Siegel 1987
T. macrura	Antarctic Peninsula	3+	1+	1+	Siegel 1987
E. superba	Antarctic Peninsula	5+	2+ F, 3+ M	2+ F, 3+ M	Siegel and Loeb 1994
E. superba	Antarctic Peninsula	5+			Kawaguchi et al. 1997
E. superba	Antarctic Scotia Sea	6–7 years			Rosenberg et al. 1986
E. superba	Antarctic Indian Ocean	5+			Aseev 1984
E. superba	Antarctic Indian Ocean	4+	3+ F, 3+ M	3+ F, 3+ M	Hosie et al. 1988
E. superba	Antarctic Indian Ocean	4+	3+	3+	Pakhomov 1995*a*
E. superba	Antarctic Indian Ocean	5+			Wang et al. 1995
E. superba	Antarctic Indian Ocean	5+			Lu and Wang 1996
E. superba	Antarctic Indian Ocean	6+	0 = larvae, 1+ = juveniles		Ettershank 1985

Note: M, males; F, females; R, recruits.

was again found that spawning of high-latitude species is coupled with the onset of the phytoplankton bloom (Einarsson 1945; Astthorsson and Gislason 1997).

Thysanoessa raschii overwinters partially on its stored lipid, but it also seems to rely on omnivorous feeding throughout the year. It reproduces later and for a more prolonged period than *T. inermis* (Hopkins et al. 1984), suggesting that spawning in *T. raschii* is tied to ambient food supplies. The larger size of Bering Sea krill observed by Smith (1991) in warm years is presumably simply caused by a prolonged production and, consequently, growth season. Similar to growth, the timing of the spawning season in high-latitude euphausiids is probably not temperature dependent but related to seasonal resource limitation (growth) or food availability (spawning) (Clarke and Peck 1991).

The spawning season of *E. superba* is limited to the Antarctic summer and the species is the last in a row of Antarctic euphausiids, starting in late winter with the more mesopelagic and (or) carnivorous species further north (1 September for *T. macrura* and *Euphausia triacantha* and 1 October for *Euphausia frigida*) and ending with the more southerly epipelagic species of the seasonal and permanent pack-ice zone (1 November for *Euphausia crystallorophias* and 1 December for *E. superba*) (Siegel 1987; Menshenina 1990*b*; Hosie 1991).

Differences in the regional onset of spawning of *T. macrura* and *E. frigida* (Makarov 1979*a*, 1979*b*) or *E. superba* (Spiridonov 1995) suggest that there are not only interspecific but also intraspecific variations in latitudinal timing of Antarctic euphausiid spawning (north–south "phenological waves" in the onset of spawning). The southward progression of the phytoplankton bloom with the receding pack ice was thought to be the controlling factor for the onset of spawning. However, this does not explain the species succession in timing, with *E. crystallorophias* spawning furthest south and earlier than *E. superba*, which also might at least partly be omnivorous. Hosie (1991) indicated that *T. macrura* and *E. frigida* in the Indian Ocean could spawn under the pack ice far away from the ice edge and the associated phytoplankton bloom. The proximate causes initiating the onset of euphausiid spawning in Antarctic waters are not satisfactorily explained and certainly need further attention.

Spawning of *E. superba* has been thought to be a long process over most of the summer period from late November to late March. However, it was shown that the onset of spawning may change with geographical region (Spiridonov 1995) and varies interannually (Siegel and Loeb 1995). Spiridonov (1995) speculated that the beginning of the spawning season might be regulated by the rapidity of the pack-ice retreat in spring and the development of the phytoplankton bloom. However, from results of their long-term data set, Siegel and Loeb (1995) concluded that the winter ice extent and the duration of the ice cover influence the onset of the spawning season. After severe winter and possibly good ice-algae resources, spawning started intensely and as early as December and finished early in the season. A good example was the FIBEX season 1980–1981, during which spawning started as early as December after a severe winter and the reproductive season was more or less completed in January after less than 6–8 weeks (Siegel 1985) and that still is one of the most successful spawning events of the last two decades. Following mild winter with hardly any pack ice in the region, the krill spawning season generally starts slowly in January and lasts long into the late summer season. During these years, spawning success is minor.

Maturation and spawning

For most species, we still have no clear idea how long the different stages last from fertilized females carrying spermatophores to the final shedding of eggs. Experimental data are certainly helpful in this regard, but as it is often the case, these results may show the species' plasticity in adaptation or its behavioural flexibility and not exactly the multifactorial result under natural conditions. The development of spawning indices from natural populations should help to identify the progress in spawning over the season and allow a parameterized comparison between years of the timing of spawning.

Table 1 lists age at maturity and age at first spawning for a number of species around the world. Two basic, but demographically important, aspects become evident. Firstly, most species attain sexual maturity at a certain age, and without wasting more time (energy), they immediately start to spawn for the first time. Secondly, adults of most species seem able to participate in repetitive spawning events during their life cycle, independent of their maximum age, should the life span be as short as several months or as long as several years. Dependent on the maximum age (months or years),

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the age of first spawning will certainly be different among species and the number of repetitive spawning events during a single year will be different.

Long larval and juvenile phases are known from polar species like the Antarctic krill *E. superba*. Females do not mature before the beginning of the third summer season of life (age group 2+). Males even need another year to become mature (Siegel and Loeb 1994). During the same season of their maturation, these adult animals start to spawn for the first time. However, spawning success is more dependent on older female age groups, although these are less abundant but have a much higher fecundity. Assuming a maximum age of 5+, this would give a female the chance to spawn up to four times during its life cycle. In principle, the situation is similar in boreal species like *Thysanoessa longicaudata*. In the North Atlantic, this species attains a maximum age of 2+. As for many other temperate water species, maturation and first spawning occur at the age of 1+ and females spawn during a second breeding cycle at 2+ (Einarsson 1945). Off northern Iceland, conditions for this species seem to be less favourable and it does not survive to the age of 2+ (Astthorson and Gislason 1997) so that the spawning stock consists of only one age-class.

With their distribution from boreal to arctic regions in the Atlantic as well as the Pacific, the species *T. inermis* and *T. raschii* cover a large latitudinal range and quite different oceanographic conditions. Their spawning and maturation timing show some peculiar adaptations (see Table 1). At their southern distribution limits, the two species attain a maximum age of 1 year, during which they mature, spawn, and die after the first spawning season. In boreal waters around Scotland, Iceland, western Norway, and Nova Scotia, the maximum age of the species increases to 2 years. Age at maturity and age at first spawning still occur at the age of 1+, with the consequence that part of the population survives for another year and spawns for a second time. In subarctic waters off northern Norway, the species further demonstrate their plasticity in age structure and maturity development. Maximum age is still 2+, and most males become mature as 1-year-olds; however, very few females spawn at the age of 1+ and therefore only spawn once at the age of 2+ (Falk-Petersen and Hopkins 1981). This trend continues in the Barents Sea and for the Pacific in the southeastern Aleutians region, where individual krill reach a maximum age of 3+ (Nemoto 1957; Lindley 1980). Here, they do not mature and spawn before the age of 2+. However, the number of second-time spawners at the age of 3+ must be very low because several authors did not record this oldest age-class (see Table 2). Greenland and the northeastern Aleutians are probably the most extreme and still acceptable habitat because the species need 3 years to reach maturity and spawn for a single season. Further north in High Arctic waters, they still mature, but successful spawning no longer occurs and the populations have to be replaced by advection from the south.

Euphausia pacifica is another more flexible species in its timing of maturation. In the North Pacific, it reaches maturity at age 1 and has a maximum life expectancy of 2 years. *Euphausia pacifica* spawns only once a year in the Bering Sea with a peak in mid-June. Strict seasonality in the high-latitude populations of *E. pacifica* seems to have the advantage of leading to increased size uniformity and breeding efficiency during the spring bloom (Brinton 1976). A second spawning occurs at the age of 2 and a mean length of 15 mm (Ponomareva 1963). Single spawning events once a year are also reported from Japan and Kamchatka. Spawning around southern Japan takes place in spring, but minimum maturation size is not reached before the following February at a size of 11–12 mm. Maximum age is at least 15 months but less than 21 months, so an adult female is only reproducing once during its life time and only one generation is produced every year (Iguchi et al. 1993). An interesting phenomenon is described for *E. pacifica* around northern Japan similar to *Thysanoessa* spp. off northern Norway, where maximum age increases with latitude and an intermediate step of retarded maturation occurs. *Euphausia pacifica* of northern Japan takes a slightly different step; here, both sexes reach maturity and spawn at age 1+, but only females survive for another season and spawn a second time at age 2+ (Nicol and Endo 1997), indicating the flexibility of the species to adapt to latitudinal changes.

The same species shows a very different behaviour off the coast of California where calyptopis larvae occur year-round with three to four maxima within a year, indicating pulses of spawning every 2 months (Brinton 1976). Here, the short-lived but fast-growing spring cohorts already mature after 4 months, whereas the fall recruits show a retarded growth over winter and need about 7 months for maturation. However, these pulses are of different productivity (egg and larvae densities) and quality (growth rate and survivorship); the highest calyptopis larval peak off the California coast is in May–August during the main upwelling period and off Oregon's coast is in August–December in response to summer upwelling (Bollens et al. 1992). Similar observations are reported from upwelling areas off British Columbia's coast, with up to six spawning events each year but with little success during the winter period (Tanasichuk 1998*b*). Although six breeding events per year comes close to continuous spawning, it was emphasized that spawnings by *E. pacifica* are discrete events and thus have a cohort/age structure.

In short-lived species, spawning generally occurs several times during the course of a year or even leads to continuous breeding. The seasonal spawning events often have a cohort structure and can be followed over the entire life span of the species, which rarely extends over more than 1 year. These are found preferably in warm or temperate waters such as the more oceanic *Euphausia eximia*. This species has a maturation time (7 months) similar to that of *E. pacifica* autumn cohorts, while the subtropical coastal species *Nyctiphanes simplex* has a very short developmental time. Obviously, *N. simplex* takes great advantage of the productive upwelling, and after 1–2 months, it already attains sexual maturity. The adult phase is thought to last between 6 and 7 months, which is relatively long compared with a maximum life span of 9 months. With an estimated generation time of >30–63 days (Gomez 1995; Lavaniegos 1995), a female would be able to breed three to four times during its life cycle in subtropical Baja California waters with temperatures between 16 and 28°C, and several generations could be produced annually. A proportionately long reproductive life relative to the entire life span in combination with the continuous maturation and the high breeding frequency are probably advantageous in a more variable inshore environment. On the other hand, the

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Table 2. Mean length at age data (total length, mm) for different euphausiid species in different regions.

Species	Geographic region	Season	Age (years) 0	1+	2+	3+	4+	5+	Reference
T. raschii	North Atlantic, boreal	Spawning season		13	21				Einarsson 1945
T. inermis	Barents Sea	June		13.4	20.8				Dalpadado and Sjoldal 1991
T. inermis	Barents Sea	Oct.	12.1	19.8	22.5				Dalpadado and Sjoldal 1991
T. inermis	Barents Sea	Jan.	11.7	20.3	24.5				Dalpadado and Sjoldal 1991
T. inermis	Barents Sea	May		13.1	22.1	24.2			Dalpadado and Sjoldal 1991
T. inermis	Barents Sea	Oct.	9.5	12.8	17.1	22.1			Dalpadado and Sjoldal 1991
T. inermis	Barents Sea	Jan.	9.9	12.6	16.6	21.5			Dalpadado and Sjoldal 1991
T. inermis	Barents Sea	End of growth season	10.5	13.9	18.5	22.7			Dalpadado and Sjoldal 1995
M. norvegica	Scotland	Winter, range of size-classes	24–26	36–37	42–48				Mauchline 1980
M. norvegica	North Atlantic	Winter (mean total length)	18	25	32				Einarsson 1945
M. norvegica	North Atlantic	Winter (means for different years)		20–23	31–36				Lindley 1982*a*
M. norvegica	Kattegat	Winter (mean total length)	20	31	36				Boysen and Buchholz 1984
E. pacifica	Southern California	Feb. cohort after 7 months	19						Brinton 1976
E. pacifica	Southern California	June cohort after 10 months	19						Brinton 1976
E. pacifica	Southern California	First spawning	11.5						Brinton 1976
E. pacifica	Southern California	Second spawning	16						Brinton 1976
E. pacifica	Southern California	Third spawning	20						Brinton 1976
E. pacifica	Oregon	Sept. cohort after 13 months		22					Smiles and Pearcy 1971
E. pacifica	Southern Japan	0 age group in winter, 1+ at 21 months	10	20					Iguchi et al. 1993
E. pacifica	Northwest Pacific	Spring		13–14	19				Ponomareva 1963
E. pacifica	Northwest Pacific			17–18	22				Nemoto 1957
E. pacifica	Northeastern Japan	0 age group in winter, 1+ in summer	10–12	16–18					Taki and Ogishima 1997
E. superba	Antarctic Peninsula	Feb.–Mar.	3–8.5	29.0–31.8	38.0–41.3	45.5–47.6	51.0–52.3	55.5–57.1	Siegel 1986
E. superba	Antarctic Peninsula	Mar.–Apr.	8.0	30.0	39.4	44.5	50.0		Siegel 1987
E. superba	Antarctic Peninsula	May–June	6.7	28.7	36.0	43.6	50.3	54.2	Siegel 1987
E. superba	Antarctic Peninsula	Oct. (spring)	12.7	30.5	40.0	46.0			Siegel 1987
E. superba	Antarctic, Weddell Sea	Jan.–Mar. (summer)	1.0–2.0	20.8–25.2	39.2	44.5	50.1		Siegel 1987
E. superba	Antarctic, Weddell Sea	Oct.–Nov. (winter–spring)		26.4	39.3	44.8			Siegel 1987
E. superba	Antarctic, Indian Ocean	Dec.–Mar.		29.6–32.2	37.4–38.3	43.4–44.8	47.8–50.7	52.4–55.4	Aseev 1984
E. superba	Antarctic, Indian Ocean	Dec.–Feb.	1.2–7.3	19.0–30.8	34.2–40.9	41.2–48.8	51.0–54.9		Hosie et al. 1988
E. superba	Antarctic, Indian Ocean	Jan.–Feb.		22.3–28.4	39.0–41.8	44.2–46.4	49.2–51.5	54.8	Wang et al. 1995
E. superba	Antarctic, Indian Ocean	Mar.–Apr.		25.7–30.6	32.8–40.7	40.3–48.3	49.2–55.0		Pakhomov 1995*a*
E. superba	Antarctic, Indian Ocean			28.4	41.8	46.4	50.3	54.8	Lu and Wang 1996
E. frigida	Antarctic Peninsula	Jan.–Mar. (summer)	12.3	17.8					Siegel 1987
E. triacantha	Antarctic Peninsula	Jan.–Mar. (summer–fall)	19.1	27.9	34.0				Siegel 1987
E. crystallorophias	Antarctic Peninsula	Jan.–Mar. (summer–fall)	7.0*	18.3–19.3	25.4–26.4	30.0–32.1	35.9		Siegel 1987
T. macrura	Antarctic Peninsula	Jan.–Mar. (summer–fall)	6.3	17.1–19.9	22.3–23.6	27.3–29.4			Siegel 1987

*According to Fevolden (1980) from the Weddell Sea at the end of February.

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postponed age at maturity observed in subtropical *E. eximia* helps this species to maintain a stable population in an offshore region that is less productive but less variable.

Euphausia hanseni (Benguela Current) almost continuously breeds throughout the year (14 times in 6 months), with few relatively large eggs released into the sea. *Nyctiphanes capensis* shows a lower frequency of spawning, with a large number of small eggs protected in a brood pouch (Barange and Stuart 1991). These authors argued that both strategies allow these short-lived species to maintain a relatively high stock density in a fluctuating physical environment.

Euphausia lucens, the third important species of the Benguela Current system, appears to have two periods of intensive spawning throughout the year in inshore waters, while further offshore intense breeding occurred at least three times a year or happened almost continuously. The ovaries of the species contain a large size range of eggs of different stages, indicating the production of multiple broods in the individual female (Pillar and Stuart 1988). Assuming a life span of 9 months for the adult stage, females would reproduce between three times in inshore waters and nine times in offshore waters. However, from an energetics point of view, with a substantial loss of lipid after spawning as well as the high loss of body carbon for the individual female krill during repetitive spawning events (Ross et al. 1982), it seems unlikely that such high rates of egg production can be sustainable for the female over such a long period.

Development of eggs and larvae

After spawning, euphausiid eggs are fertilized and depending on the genus are liberated into the water or are carried attached to the underside of the female on the posterior thoracic limbs after she has laid them. The attachment method offers protection by the female against inter- and intra-specific predation at least until the larvae hatch and prevents a wider geographical dispersion. The free-release method allows the production of a huge number of offspring but includes the risk of the eggs sinking to the bottom if they are heavy. Alternatively, if the eggs are neutrally buoyant, they risk predation by the parental stock or other plankton feeders. Species like nearshore upwelling *Nyctiphanes* spp. carry their eggs in brood pouches until the metanauplius stage or they release neutrally buoyant eggs. Species concentrating or spawning in the vicinity of the shelf break seem to prefer eggs heavier than seawater, which sink during their development beyond the main vertical distribution range of the parental stock.

Euphausia pacifica spawns in the surface layer and eggs seem to be neutrally buoyant and occur in the upper 50 m of the water column during day and night. Vertical migration of the parental stock for feeding could create a negative effect on the survival of the eggs and early larval stages. One could argue that the vertical migration of adults might reduce the problem when they migrate into different current layers of different direction or velocity and reduce the predation pressure on their own offspring. In areas where differential transport of adults and eggs and larvae is not efficient, the larval mortality might be a function of adult stock density.

The neritic Antarctic *E. crystallorophias* shows a maximum concentration of the earliest stages in the upper 25 m of the water column (Makarov 1979*b*). This layer also belongs to the preferred habitat for the parental stock, and with its homogeneous vertical structure of the water masses, strong undercurrents are hardly to be expected to segregate adult filter feeders and their early life stages sufficiently to avoid serious predation pressure. The problem is more or less solved by *E. superba*'s negatively buoyant eggs, which are rapidly sinking below the major depth range of the spawning stock occurrence.

Eggs of *M. norvegica* and *T. raschii* were reported to sink at a speed of 5 $m \cdot h^{-1}$ (Mauchline and Fisher 1969). With a developmental time of 10 days to hatching of the nauplius, this could cause increased mortality rates in shallow-water areas because eggs of *T. inermis* then reach the bottom of the North Sea in 24 h (Lindley and Williams 1980). Either sinking rates of eggs for these shelf species are estimated to be high or survivorship is low and the stock has to be recruited from somewhere else.

Sinking rates of Antarctic krill eggs were measured in the laboratory. Mean values ranged from 195 $m \cdot day^{-1}$ for the first 24 h and 95 $m \cdot day^{-1}$ after 36 h (Ross and Quetin 1982) to 220 $m \cdot day^{-1}$ (Marschall 1983). Assuming an average 5-day developmental time for krill eggs, hatching of eggs should occur between <700 and 1350 m. Until these studies had been performed, only few eggs had been caught, but all in deeper water than the experiments were predicting. One hypothesis suggested that krill eggs are fragile and that the few eggs found in net samples may not represent the true abundance in nature.

However, Hempel and Hempel (1986) reported successful deep tows for krill eggs and larvae in the Scotia Sea that yielded more than 66 000 eggs and nauplii per 1000 m^3 in the 1000- to 2000-m layer, with few eggs deeper than 2000 m, but hardly any in the water column above 1000 m. Trying to explain the discrepancy between these field observations and the experimental sinking rates for eggs, Hempel and Hempel (1986) speculated that gravid krill may dive deep and spawn in mesopelagic depth layers. However, there are no field data supporting this behaviour, and deep stratified tows down to 1000 m never yielded gravid krill beyond 400 m depth at any noteworthy concentrations (V. Siegel, unpublished data). A deep vertical spawning migration does not seem necessary because other authors reported on egg developmental times of up to 8 days instead of only 5 days (Ikeda 1984; Mauchline 1980), which would add another 285–660 m to the theoretical maximum sinking depth of 700–950 m. This adjustment of basic assumptions alone would explain the main occurrence of krill eggs in 1000- to 2000-m depth strata.

From the data that Hempel and Hempel (1986) presented, it appears that nauplii are still sinking until the metanauplius finally starts its upward migration. According to the data in Table 3*a*, this would give the metanauplius a little more than 10 days to accomplish the full ascent because after about 30 days from spawning, the calyptopis I (C1) stage reaches the near-surface layers. C1 is the first feeding stage and performs diel vertical migration as all older larval stages do. However, feeding is critical for this larval stage because it can only survive for a maximum of 6 days without food (Ikeda 1984).

Thysanoessa macrura performs a vertical ontogenetic migration similar to that of *E. superba*, although eggs do not

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seem to sink as deep. Nauplii and metanauplii are primarily recorded from the 500- to 1000-m layer. A large number of C1 are still found in this deep layer, whereas C2 and C3 are concentrated in the upper 200 m. There is also a latitudinal difference for the older stages; the 200-m surface layer is preferentially populated by larvae in more northern waters of the distribution range, while in the south, they are restricted to the upper 100 m. Similar ontogenetic migrations were also reported for *E. pacifica* in waters off Japan, where surface-spawned eggs sink to 600 m depth before they hatch and reoccur at the surface as the calyptopis stage. Consequently, the well-known "developmental ascent" of larvae from their deepwater hatching zone to the photic layer is not unique to *E. superba* but is obviously a common adaptation in other species with species-specific sinking rates and hatching depths as mentioned above with the exception of the neritic *E. crystallorophias*.

Developmental pathways

In euphausiid species, a nauplius (N) hatches from the egg and then passes through a metanauplius, three calyptopis, and multiple furcilia (F) stages before it reaches the juvenile phase. For most species, three calyptopis stages have been described, while the number of furcilia stages varies, e.g., six for *E. superba* and seven for *E. pacifica*. After a detailed study of larval development, Suh et al. (1993) found that the main characteristic separating F5 from other stages (the segmentation of antennal endopods in the fifth furcilia form) is not reliable for practical identification, and they concluded that there are only six instead of seven furcilia stages. In light of these results, the eight furcilia stages of *E. crystallorophias* (Menshenina 1990*a*) may need verification.

Most species investigated under this aspect show different possible developmental pathways during larval growth. Off South Africa's coasts, six furcilia stages are known for *E. lucens*, but two main pathways are followed in its ontogenetic pleopod development. In these cases, a setose pleopod appears where a nonsetose pleopod existed before. Although the developmental pathways of *E. lucens* seemed to be independent of diet, it is thought that trophic conditions or environmental factors like temperature strongly affect the number of moults as well as the number of forms and consequently additional possible pathways in larval development (Pillar 1984). According to this author, coastal populations have more variable pleopod development than oceanic populations, which have relatively stable and well-defined forms.

Dominant pathways of larval development in *M. norvegica* and *E. pacifica* seem to be affected by temperature and particularly quantity and quality of food (Suh et al. 1993). It is suggested that under favourable conditions, the number of instars is reduced and the development of appendages is accelerated.

The Antarctic krill *E. superba* is found in the Scotia Sea in water bodies of different origin. Like in other species, changes in dominance occur and are accompanied by deviations in other, parallel developmental pathways. For *E. superba*, form 5′ represents the main dominant form in the ontogenesis in Antarctic Circumpolar Current waters. However, data from pure Weddell Sea water showed that form 5′ was completely absent. Differences in proximate causes like water temperature or food availability should increase the variability of the larval forms becoming evident in an increase in other developmental pathways. However, according to Makarov and Maslennikov (1981), the complete absence of the dominant form cannot be explained by a change in developmental pathways alone because a disappearance should be temporary. Therefore, they concluded that the absence of form 5′ indicates the existence of at least a subunit of a population or two physiological races breeding on either side of the Weddell–Scotia Confluence.

Examples on size of larval stages are given in Table 3*b*. Mean size of larval stages in a given area was often reported to be very consistent between years (e.g., Tanasichuk 1998*a*, 1998*b*). Unfavourable conditions seem to more greatly influence the moulting frequency and the duration of larval stages but not the mean size of each stage. However, some geographical variation in the mean size of stages was reported for *E. pacifica* in the western and eastern Pacific (Suh et al. 1993).

Developmental times were determined from the *E. superba* egg to the N1 stage. The results deviated substantially: 3–4 days at 1.5°C (McWhinnie and Denys 1978), 5–6 days at 0–1°C (Ross and Quetin 1982), 7 days at 0.4°C (Kikuno 1982), and 8 days at 0°C (Ikeda 1984). The temperature effect on the developmental time is therefore quite evident.

Duration of *E. superba* calyptopis stages from field samples was on average 12.5 ± 0.9 days, which was similar to the duration of furcilia stages, i.e., 13.1 ± 0.9 days (Menshenina and Spiridonov 1991). Antarctic species in general show a fairly constant time range for the development of larval stages. The development time of the more northern and mesopelagic *E. frigida* calyptopis and furcilia stages from field samples was on average 13 days, of *E. triacantha* between 15 and 18 days, of the high-latitude shelf species *E. crystallorophias* no more than 16 days, and of the oceanic epipelagic *Thysanoessa* between 10 and 16 days (Menshenina and Spiridonov 1991).

Total time of development for *E. superba* up to the F6 stage takes a minimum of 116–135 days (Ikeda 1984; Mauchline 1980) and 240 days maximum according to field samples (Witek et al. 1980). Winter surveys reported F3–F5 from June, but F6 did not predominate before August (Daly 1991), which was at least 150–180 days after the eggs had been spawned. The experimental data seem to reflect more the potential for the species' larval development.

Even longer developmental times have been described for the high-latitude Antarctic species *E. crystallorophias*. First occurrence of eggs was recorded from November. Rearing experiments (Ikeda 1986) and year-round field samples (Kirkwood 1996) showed remarkably similar results in the sense that it takes about 236 days for the larvae to reach the F6 stage, which did not occur in the plankton samples before early August. Menshenina and Spiridonov (1991) related the long larval duration to low water temperatures and argued that slow larval development is an adaptation of a cold-water stenothermic species. Poor feeding conditions in the ice-covered habitat during most of the year might be another reason for the observed long developmental time; however, during Ikeda's (1986) experiments, *E. crystallorophias* showed the same slow rates, despite abundant food supply. Interest-

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Table 3. Cumulative developmental times for and mean or range of length-classes of larval stages of different euphausiid species.

(*a*) Developmental time (days).

	E. superba					
Larval stage	Ikeda 1984	Mauchline 1980	Witek et al. 1980	*E. crystallorophias* (Ikeda 1986)	*E. pacifica* (Ross 1981)	*T. inermis* (Lindley and Williams 1980)
Egg	0	0	0	0		0
N1	8	8		10	0	10
N2	13	17				
Metanauplius	20	25		27	2.0–2.2	
C1	30	34	30	34	4.5–8.0	
C2	44	44	45–60	54	10.0–13.5	24–33
C3	53	53	60–75	67	14.0–18.5	
F1	63	63	70–90	89	17.5–22.0	
F2	75	73	75–105	100	23.0–31.0	
F3	86	84	90–120	125	27.5–38.5	31–40
F4	99	94	105–135	159	33.0–50.0	
F5	112	105	120–160	180		
F6	127	116	135–240	236	36.5–55.0	
F7?					40.0–60.0	
Juvenile					45.0–68.0	

(*b*) Length (mm).

	E. superba							
	Ikeda 1984	Fraser 1936	*E. frigida* (Makarov 1980)	*E. triacantha* (Makarov 1980)	*E. crystallorophias* (Ikeda 1986)	*T. macrura* (Makarov 1980)	*E. pacifica* (Suh et al. 1993)	*T. inermis* (Lindley and Williams 1980)
Egg	0.57	0.60			0.6		0.58	
N1	0.70	0.65	0.49–0.55		0.58	0.42–0.50	0.38	
N2	0.78	0.67					0.52	
Metanauplius	0.91	0.95	0.45–0.52†	0.67–0.73*	0.69	0.45–0.50*	0.58	
C1	1.72	1.71	0.9–1.1	0.9–1.0	1.42	1.0–1.4	0.93	1.0
C2	2.90	2.71	1.5–1.9	1.9–2.3	2.22	1.7–2.8	1.39	2.0
C3	4.26	4.01	2.5–2.9	3.0–3.6	3.56	2.9–3.1	1.92	2.5
F1	5.38	5.40	3.8–4.3	4.0–6.5	4.72	3.0–4.7	2.26	2.9
F2	6.65	6.22	4.7–5.7	6.3–7.7	6.31	3.3–4.7	3.02	3.3
F3	8.24	7.32	5.5–6.7	6.5–9.2	7.8†	3.8–4.6	3.59	3.7
F4	8.82	8.01	6.5–7.7	7.5–10.2	7.9†	4.0–4.8	4.11	4.5
F5	9.60	9.52	7.0–8.3	8.8–11.7	8.6†	4.6–5.9	4.58	4.9
F6	10.66	11.34	6.8–9.6	8.5–11.4	10.5†	5.2–6.7	5.36	5.5
F7					11.4†			

*Metanauplius stage from Makarov (1980) data set given as carapace length.
†Data from Menshenina (1990).

ingly, *E. crystallorophias* has similar spawning and developmental times at widely separated geographic locations, e.g., off the Antarctic Peninsula, in the Weddell Sea, and in the Indian Ocean.

A temperature effect on larval development rates was described by Iguchi and Ikeda (1994) for *E. pacifica*. The time required to reach the C1 stage was approximately 12 days at 5°C but only 3 days at 20°C. For the entire larval cycle, Ross (1981) found a developmental time at the end of the furcilia phase of 40 and 60 days, respectively, influenced by a temperature difference of only 4°C. This is considerably longer than the 29 days reported for field samples of *E. pacifica* off California's coast (Brinton 1976). In this example, krill larvae seem to develop faster under favourable natural conditions than during the rearing experiments. During experiments carried out with *E. superba*, a constant food supply was thought to have led to shorter development times, while in addition to temperature effects, decreasing food supply in early autumn could put another burden on the larvae. This may indicate that under natural conditions, larval development may take longer than the experimental data for *E. superba* suggest and be retarded by seasonal factors, which would also explain the wide range of results listed by Witek et al. (1980) for single larval stages (see Table 3*a*).

Age composition of postlarval krill populations

A common approach to estimating the maximum life span of a species has been a simple modal progression analysis, which follows the progression of the peaks along the length axis in a series of length–frequency samples sequentially arranged in time. This works for species with few cohorts and a relatively high growth rate and was successfully carried

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out for *T. inermis*, *T. raschii*, and *E. pacifica* (e.g., Einarsson 1945; Bollens et al. 1992).

Despite frequent criticism, methods using analyses of length data have found wide application in the determination of species' age and growth. Statistical methods applied to distribution mixtures were first successfully used for Antarctic krill by Aseev (1984) (graphical method on probability paper) and Siegel (1986, 1987). These authors found a much longer life span for this species than the formerly thought 2-year life cycle (Mauchline and Fisher 1969) (Table 1). Analyses from other studies and areas in principal confirmed the results of a multiyear life cycle (Hosie et al. 1988; Pakhomov 1995*a*; Wang et al. 1995). Table 2 shows the suprisingly similar results on length at age data from various sources around the Antarctic continent. Whether there are age-classes beyond 5+ for Antarctic krill cannot be resolved with the present methods. Age groups beyond 3+ strongly overlap so that they are difficult to separate under conditions when all age-classes are present in relatively high numbers. The analysis is much easier when single age-classes are underrepresented due to recruitment failure and creates a much clearer picture of the size distribution pattern of the remaining age groups. The detailed work of Lu and Wang (1996) on the separation of distribution mixtures demonstrates that a high increase in the significance level of the fit is possible when assuming the existence of a 5+ age group instead of a maximum age of 4+. It is also evident that the mean length at age for the younger age-classes is very stable and the results are very robust whether the procedure includes or excludes a 5+ age group. In this case, only the mean length of the 4+ group is obviously affected. At the same time, the frequency of the 5+ age group is already <1% of the stock size so that even older age groups would not substantially contribute to the population or strongly influence population dynamic parameters.

The two sympatric species *T. inermis* and *T. raschii* have a wide boreal to low arctic distribution. Due to their wide latitudinal range, these species show an interesting succession of population age structures (also see Maturation and spawning section above). At their southern distribution limits, *T. inermis* and *T. raschii* attain a maximum age of 1 during which they mature, spawn, and die. In temperate waters around Scotland, Iceland, western Norway, and Nova Scotia, part of the population survives for another year. In subarctic waters off northern Norway, the maximum age is generally 2+. In the Barents Sea, off Greenland, and in the eastern Aleutians region, individual krill reach a maximum age of 3+. Further north in high arctic waters, they still survive sporadically as expatriates, but spawning no longer occurs.

Well-documented mean length at age data for these species are only available from Barents Sea studies (Table 2). Although Einarsson (1945) did not identify the 3+ age group, his mean length at age data from *Thysanoessa* krill in the North Atlantic regions are very similar to the findings of Dalpadado and Skjoldal (1991, 1995) for the Barents Sea. Obviously, the species change their maximum age with latitude, but not their length at age, although records exist that *Thysanoessa* grow to a larger maximum size close to their northern distribution limits. Additional data from other regions are needed for a better interpretation of the latitudinal response of the species on mean length of age groups.

Meganyctiphanes norvegica has a more boreal distribution range in the Atlantic than the latter two species. In the Mediterranean Sea, it has a maximum life expectancy of 1 year and a single spawning season during its life cycle. In waters off western Norway, the species lives to an age of 2+. Differently from *Thysanoessa* spp., the maximum age of *M. norvegica* does not increase off northern Norway and in the southern Barents Sea; it still is documented as 2 years and 6 months, but it does not spawn here and is advected into these northern regions by the North Atlantic Current (Falk-Petersen and Hopkins 1981; Drobysheva 1987). The stock therefore largely depends on the immigration of individuals transported from the south. Data from northern Iceland very much resemble the situation in the Barents Sea (Astthorsson and Gislason 1997). Although the mean length at age for most areas seems to be consistent, results on mean length for older age-classes seem to be higher for Scottish and Norwegian waters (Table 2). However, these geographical differences were not confirmed by Lindley (1982*a*), and further data and considerations are likely needed. On the other hand, it is noteworthy that the same author recorded mean length at age data from the North Atlantic for different years and these show only minor interannual differences.

Euphausia pacifica, like the North Atlantic *Thysanoessa* spp., is another example of large geographical variation in maximum age. These species experience the shortest life span of 6–8 months along the coast of California, which is the southernmost distribution limit. After 4 months, the spring recruits reach maturity. In the same area, the autumn cohorts survive to an age of 10–13 months. However, the maximum size of the different cohorts is very similar (Brinton 1976). On the western side of the Pacific in Japanese waters, the maximum age of *E. pacifica* slightly increases to 15–21 months. Off the coasts of Oregon and Washington, longevity is similar to that in Japanese waters and mean length at age for 0+ and 1+ krill is comparable on both sides of the Pacific (Smiles and Pearcy 1971; Iguchi et al. 1993). At higher latitudes (Aleutians, Kamchatka), part of the population survives the following winter and reaches an age of 2+. Although the maximum size of the species seems to be similar for most of the distribution range, the mean length at age in high-latitude regions is obviously smaller. The mean length of 1+ krill off Oregon and Japan was about 20–22 mm, whereas the populations reach only 13–18 mm in the northern regions and need another year to gain 19–22 mm mean length as the 2+ age group.

Different species spend varying proportions of their lives in a phase of growth prior to reproduction. The boreal species *T. raschii*, *T. inermis*, and *M. norvegica* spend about 40% of their maximum life span for growth before they start to spawn for the first time. Outside their distribution centres, this proportion increases to almost 90% for *Thysanoessa* spp. in the Barents Sea and off Greenland and to more than 70% for *M. norvegica* in the Mediterranean. The Antarctic krill *E. superba* and the oceanic species *T. longicaudata* in the central North Atlantic and *E. pacifica* in the central North Pacific all show similarly low proportions (36–40%) of prereproductive lifetimes. The length of the phase for growth increases to 50% of the maximum lifetime for *E. pacifica* at the fringes of its distribution range around Japan and off California for the spring recruits. The fall recruits

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Table 4. Natural mortality rates (M) of euphausiids. In some cases, M was calculated from data published in the cited reference.

Species	Geographic region	Age group or developmental stage	M (year^{-1})	Method	Reference
E. pacifica	California	Larvae, 0+	1.83*		Calculated from Brinton 1976
E. pacifica	California	Juvenile, 0+	0.40*		Calculated from Brinton 1976
E. pacifica	California	Adult, 0+	0.51*		Calculated from Brinton 1976
E. pacifica	California	Lifetime	3.00		cf. Jarre-Teichmann 1996
E. pacifica	Oregon	Lifetime	8.70		cf. Jarre-Teichmann 1996
E. pacifica	British Columbia, Canada	Lifetime	0.60–1.90		cf. Jarre-Teichmann 1996
Thysanoessa spp.	Barents Sea	0+	3.90		Calculated from Drobysheva 1987
Thysanoessa spp.	Barents Sea	1+	0.69		Calculated from Drobysheva 1987
T. inermis	North Atlantic	2+	0.80		Lindley 1980
T. raschii	Scotland	1+	1.39		Mauchline and Fisher 1969
M. norvegica	Scotland	1+	0.69		Mauchline and Fisher 1969
M. norvegica	Scotland	2+	2.30–3.00		Mauchline and Fisher 1969
E. superba	Antarctic Peninsula	Postlarvae	0.78–1.17	Linearized catch curve	Siegel 1986
E. superba	Antarctic Peninsula	Postlarvae	0.88–0.96	Linearized catch curve	Siegel 1992
E. superba	Antarctic Peninsula	Postlarvae	0.66–0.92	Alagajara, max. age: M	Siegel 1992
E. superba	Antarctic Peninsula	Postlarvae	0.94–0.99	Pauly, VBGF: M	Siegel 1986
E. superba	Antarctic, Scotia Sea	Postlarvae	0.81–1.35	VBGF k: M	Priddle et al. 1988
E. superba	Antarctic, Scotia Sea	Postlarvae	0.5	One cumulative length–frequency	Basson and Beddington 1989
E. superba	Antarctic, Scotia Sea	Postlarvae	0.45–0.65	Length-dependent predation curve	Basson and Beddington 1989
E. superba	Antarctic Peninsula	Postlarvae	0.38–1.22	VBGF: M; max. age: M	Basson 1994
E. superba	Antarctic, Indian Ocean	Postlarvae	0.52–0.57	Richter and Efanov	Pakhomov 1995*a*
E. superba	Antarctic, Indian Ocean	Postlarvae	0.72–0.87	Alverson and Carney	Pakhomov 1995*a*
E. superba	Antarctic, Indian Ocean	Postlarvae	0.76–2.92	Beverton and Holt	Pakhomov 1995*a*
E. superba	Antarctic, Indian Ocean	Year 1	1.09	Zikov and Slepokurov	Pakhomov 1995*a*
E. superba	Antarctic, Indian Ocean	Year 2	0.65	Zikov and Slepokurov	Pakhomov 1995*a*
E. superba	Antarctic, Indian Ocean	Year 3	0.57	Zikov and Slepokurov	Pakhomov 1995*a*
E. superba	Antarctic, Indian Ocean	Year 4	0.77	Zikov and Slepokurov	Pakhomov 1995*a*
E. superba	Antarctic, Indian Ocean	Year 5	1.54	Zikov and Slepokurov	Pakhomov 1995*a*
E. superba	Antarctic, Indian Ocean	Year 6	2.41	Zikov and Slepokurov	Pakhomov 1995*a*

Note: VBGF, von Bertalanffy growth function.
*Per month.

developing over winter even require 70% of their entire life to reach the reproductive phase. One of the shortest growth periods is found in *N. simplex* from western Mexico; it ranges from 13% in the south, closer to its distribution centre, to 23% in more northern waters.

It seems as if the species have their shortest proportional growth phase in the vicinity of their central distribution range, independent of boreal, polar, or tropical environments. Maximum life span and repetitive spawning indicate a prolonged adult phase, which has the advantage of a high fecundity per female over its lifetime. Closer to the distribution limits, euphausiid species seem to spend proportionately more time for growth and less for reproduction.

Population processes, gains, and losses

Natural mortality

It is a well-established fact that mortality in planktonic larvae of marine organisms is extremely high. Since this mortality rate affects the spawning success and the later population size, knowledge of mortality rates and their proximate causes is important. However, quantitative data on larval mortality in euphausiids are still scarce. The few examples given below demonstrate how rudimentary these results still are.

During experiments, the highest mortality in *E. pacifica* occurs at the time when nauplii moult into C1 and when calyptopis moult into furcilia. After the F3 stage, the survival rate is relatively high and constant (Ross 1981). Mortality rates estimated from field samples are high for *E. pacifica* larvae in Californian waters. Brinton (1976) estimated that only 16% of the larvae survive per month. After the short larval phase, the mortality rate is lower, about 67% of the juveniles to adults survive per month, but mortality increases again after spawning and adult survival is only about 60%·month^{-1} for the adults until the next spawning event. Differences in mortality rates were observed for recruits from different spawning periods. July–December recruits live longer and also have a higher survival rate (50–60%·month^{-1}), while February–June recruits grow more rapidly but live shorter and face a lower survival rate (26–45%·month^{-1}). In *T. inermis*, mortality is about 93–97% for early larvae from the egg to the furcilia stage (Lindley and Williams 1980) and very similar to *T. raschii* with 97% (Lindley 1980) and *T. longicaudata* with 98% (Lindley 1978).

Quantitative estimates of natural postlarval mortality M are also rare in the published literature on euphausiid species

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(Table 4). Several values of M for *E. pacifica* are given in Jarre-Teichmann (1996), with $M = 3.0 \cdot year^{-1}$ off California, $M = 8.7 \cdot year^{-1}$ for Oregon, and $M = 0.6–1.9 \cdot year^{-1}$ for British Columbia. These differences are difficult to explain, although the maximum life span is different in these areas. As expected, the lowest mortality rate is seen for animals living for 19–22 months off British Columbia. However, stocks off Oregon and California reach the same maximum age of about 1, but their life cycle is different. One cohort is reproducing about three times during its life off California but seems to reproduce only once off Oregon, for which a much lower mortality rate would be expected.

Mortality of *Thysanoessa* spp. in the Barents Sea is lowest in winter, when the feeding pressure of the main predator stock (cod and capelin) is minimal. The 0+ age group has the highest summer growth rate but also the highest mortality rate (98%). The 1+ age group shows a mortality rate of approximately 50%, which still leaves enough spawners (2+) in the next season to sustain the population. After spawning, mortality is thought to increase rapidly so that it was suspected that hardly any 2+ animals survive (Drobysheva 1987). However, Lindley (1980) found a mortality rate of $55\% \cdot year^{-1}$ for age-2+ *T. inermis*, and other studies regularly observed the presence of the 3+ age group in Barents Sea waters, although in very low numbers (Dalpadado and Skjoldal 1991, 1995, 1996). In Scottish waters, *T. raschii* shows a slightly higher mortality rate (75%) for 1-year-olds than in the Barents Sea (Mauchline and Fisher 1969).

Estimations of mortality rates for *E. superba* have been carried out using different methods (see Table 4). Mortality estimates vary between 0.38 and 5.5 for the postlarval population. However, the main drawbacks of some approaches were the serious underestimation of krill age. Since natural mortality is a function of maximum age, this underestimation of longevity led to the highest values in the range mentioned above. Mortality is inversely related to the longevity of the individuals of the population and hence to the growth constant parameter k of the von Bertalanffy growth function. High growth rates are usually associated with high mortality rates and low growth rates with low mortality rates so that the ratio M/k is approximately constant for a given species. For a large range of fish species, M/k lies between 1.5 and 2.5. Preliminary estimates if M/k for Euphausiacea range from 1.5 to 2.5 (based on Pauly's regression equation) and between 0.83 and 1.67 for *E. superba* obtained from maximum age calculations (for details, see Basson 1994). The range of M for *E. superba* from both approaches is 0.38–1.22. Along these lines, critical reviews of the methodology used by earlier studies (Siegel 1992; Pakhomov 1995*a*) concluded that the realistic values of M for the postlarval life cycle may range between 0.66 and 1.35.

It is also likely that mortality varies in space (between geographical regions) and time (interannually), and it is known to vary during the lifetime of a species, as already indicated for *T. inermis*. Possible differences in mortality can be attributed to differing predator demands as well as to short-term variability or long-term trends in environmental parameters. Differences in natural mortality of different developmental stages or age groups are often discussed in relation to larval food requirement, maturation, and spawning stress, and these types of data are essential in developing fisheries models. In this case, larval mortality is not of direct concern for management; the basic requirement is the estimate of mortality for those age-classes typically affected by the fishery.

Using the Zikov and Slepokurov approach (for more details, see Pakhomov 1995*b*), the estimated natural mortality rate M for *E. superba* during the first year is relatively high (1.11–1.12), decreases thereafter during the maturation period (0.52–0.65), and increases slowly for older age groups, reaching a maximum during the last year of life (1.29–2.41). These results strongly confirm the dependence of natural mortality on age. Similar studies in different regions and different years are certainly needed to evaluate the possibilities of interannual or geographical variation in mortality rates of certain age groups and consequently year-classes, leading finally also to variability in krill recruitment processes.

Production

For the understanding of the quantitative role of a species in the transfer of organic material from primary production to higher trophic levels, it is essential to interpret and compare information about krill production (Table 5).

Production to biomass (P/B) ratios

Oceanic species of temperate to warm North Atlantic waters like *Euphausia krohnii* and *Thysanoessa gregaria* breed throughout the year. These species all show a relatively high P/B ratio (5.4–6). The importance of several generations produced annually on the P/B ratio of a species was demonstrated for *T. longicaudata* (Lindley 1978). In areas where two cohorts were produced, the P/B ratio was 11.6, but the P/B ratio was not more than 2 for areas with a single generation annually. Therefore, not surprisingly, the P/B ratio is substantially higher for subtropical to temperate inshore species like *N. australis* off Tasmania and *N. simplex* off western Baja California with several generations or even almost continuous breeding (P/B ratio between 12.7 and 14). An additional factor might be seen in constant, although low, food supply, which creates a high turnover rate. Despite the fact of a relatively high P/B ratio, total net production of oceanic species remains very low (Table 5).

Results similar to those for oceanic warm water species are obtained for those species from upwelling regions like *E. pacifica* and *E. lucens*, with P/B ratios ranging between 3 and 8. Tanasichuk (1998*b*) recalculated the productivity of both species and included larvae as well as moult production and obtained total population P/B ratios of 11.5 and 16.8, respectively. The production of several generations per year and the high primary and secondary productivity of the upwelling areas are responsible for the relatively high P/B values. Closer examination of the Benguela Current species *E. lucens* has shown that in this case, the higher range of values are found for the offshore population. The high abundance of larval stages in the offshore region and their high growth rates obviously strongly influence the higher P/B values in this part of the distribution range.

The P/B indices of the common North Atlantic temperate to cold-water shelf species *M. norvegica*, *T. raschii*, and *T. inermis* are even lower and rarely exceed a P/B ratio of around 3–4, probably because they mostly spawn only once a year and annual growth rates are reduced by food-limited winter conditions. This is supported by *E. pacifica* from Ja-

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Table 5. *P/B* ratios and production for euphausiid species.

Species	Geographical region	*P/B* from growth	*P/B* total including moult	Total production (mg dry weight·m^{-2}·$year^{-1}$)	P_g (mg dry weight·m^{-3}·$year^{-1}$)	P_g (mg dry weight·m^{-2}·$year^{-1}$)	P_e (mg dry weight·m^{-2}·$year^{-1}$)	P_r (mg dry weight·m^{-2}·$year^{-1}$)	Reference
E. krohnii	North Atlantic	6.0			0.92–1.75				Lindley 1982*b*
E. lucens	Benguela Current	3.9–8.9		142.3–479.4*	77.2–185.6	77.2–185.6*	60.0–281.4*	5.1–12.4*	Stuart and Pillar 1988
E. lucens	Benguela Current			14 200 – 47 900		7 700 – 18 500	6 000 – 28 000	500–1240	Stuart and Pillar 1988
E. pacifica, adults	British Columbia	4.2–6.9		5 801 – 13 310		3 091 – 5 649	2 597 – 7 739		Tanasichuk 1998*b*
E. pacifica, all	British Columbia		10.7–23.3	9 511 – 23 402					Tanasichuk 1998*b*
E. pacifica, all, mean	British Columbia, Canada	4.5–6.9	16.8		45–165		29–93*		Tanasichuk 1998*b*
E. pacifica, larvae	British Columbia, Canada	44.2–76.8		1 659 – 12 974		1 416 – 10 769	238 – 2 205		Tanasichuk 1998*b*
E. pacifica	Japan	3.78		6550 mg C		4 117 mg C = 62.9%	1206 mg C = 18.4%	1 226 mg C = 18.7%	Iguchi and Ikeda 1999
E. superba	Antarctic Peninsula	0.83–1.1							Siegel 1992
E. superba	Antarctic, Indian Ocean	1.19–2.27							Miller et al. 1985
E. superba	Antarctic Peninsula	0.8–1.1 (5.0)	1.0–1.15	12 453 = 15.2*			2.1*		Siegel 1986
E. superba, larvae	Antarctic Peninsula	4.6							Siegel 1986
M. norvegica	North Sea, Britain	1.3–6.3			0.80–18.74				Lindley 1982*a*
N. megalops	North Atlantic	5.4			0.16–0.50				Lindley 1982*b*
N. australis	Pacific, Tasmania	14.5			78.29		25.7–41.0*	1.41*	Ritz and Hosie 1982
N. australis	Tasmania		23.1	125		78.29*	42.01*	1.41–4.22*	Hosie and Ritz 1983
N. capensis	Benguela Current			>10 000					Barange and Stuart 1991
N. couchii	Atlantic, Britain	4.0–5.5			0.67–8.23				Lindley 1982*a*
N. simplex	Baja California, Mexico	12.7	17.0	1 736	21.26	74.7%	405.9 (=23.4%)	32.89 (=1.9%)	Lavaniegos 1995
N. simplex	Baja California, Mexico	7.0				273			Gomez-Gutierrez et al. 1996
T. gregaria	North Atlantic	6.0							Lindley 1982*b*
T. inermis	North Atlantic	1.4–3.7			1.69–3.36				Lindley 1980
T. inermis	North Sea	2.9–3.3							Lindley and Williams 1980
T. longicaudata	North Atlantic	2.0–8.0			12.24				Lindley 1978
T. raschii	North Atlantic	1.3–4.1			1.54				Lindley 1980
T. spinifera, all	British Columbia, Canada		1.77–44.70	4 936 – 33 765					Tanasichuk 1998*a*
T. spinifera, adults	British Columbia, Canada	5.4–8.3	1.04–1.89	1 822 – 13 282		1 228 – 8 481	594 – 4 800		Tanasichuk 1998*a*
T. spinifera, larvae	British Columbia, Canada	41.4–112.6	13–24	1 578 – 31 943		1 369 – 25 161	210–6783		Tanasichuk 1998*a*

Note: P_g, production from growth; P_e, exuviae = moult production; P_r, egg production. The value in parentheses for *E. superba* includes larval development stages.
*Units are mg dry weight·m^{-3}·$year^{-1}$.

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pan where the species has a *P/B* ratio below 4. In contrast with the populations from the U.S. upwelling coast, *E. pacifica* in Japanese waters produces only one generation per year. Despite the difference in annual *P/B* ratios between the eastern and western coastal regions of the North Pacific, the daily *P/B* ratios are very similar between the two regions. Iguchi and Ikeda (1999) argued that the daily production rate is maintained during a much longer period of the year in U.S. waters, while the population has a much longer growth stagnation period in Japanese waters.

The lowest *P/B* ratios are found in polar species like the Antarctic krill *E. superba* for which annual production hardly exceeds the standing stock biomass. These high-latitude species all produce only one generation per year and additionally have a nongrowing season of up to 8 months. It takes the species several years of a multiyear life cycle to build up this high biomass. Temperate or warmwater species tend to have a shorter life cycle and a higher growth rate, which is reflected in the higher turnover rate and the development of several generations per year. This strongly influences the *P/B* index. The productivity of warmwater species may be similar to the values reported for Antarctic krill, but their actual stock biomass is much lower, or in other words, Antarctic krill may show high stock biomass, but due to the low turnover rate and the multiyear life cycle, this species has a relatively low productivity and the lowest *P/B* ratio.

The *P/B* values must be interpreted and compared with caution, as the actual population structure can strongly influence the results. Ritz and Hosie (1982) showed that larvae and juveniles contributed 43% to the total production of *N. australis*, while adults produced 54%. On the other hand, Lavaniegos (1995) reported that the small size-classes were responsible for 93% of the total production of *N. simplex*, probably because the size and age composition of the population was different and resulted in a much higher production rate. Similar results are described for *T. spinifera*, and Tanasichuk (1998*a*) gave four reasons why his results on *P/B* values are comparatively high compared with most other species: (*i*) other studies rarely include production other than growth, (*ii*) *T. spinifera* grows much faster than any other euphausiid species, (*iii*) exuviae production is much higher in *T. spinifera* than in other species, and (*iv*) the highest *P/B* ratios occurred in years when larvae accounted for more than 80% of the stock abundance.

The first and last points are critical when comparing *P/B* values for different species from different sources because most production estimates were confined to growth production or did not include larval stages in the production estimate. The example of *T. spinifera* clearly demonstrates that a *P/B* ratio for adults may be as high as 8.3 when including moult production but can reach 112 for the larval phase with its high growth rates. The overall ratio could then show a maximum value of around 44 including moults and larvae. Another example is the *E. superba*, a species with low production in exuviae material (see below). Therefore, the *P/B* ratio based on growth production P_g of around 0.8–1.1 does not change substantially when including exuviae production P_e (*P/B* = 1.0–1.15). However, when larval stages are considered (the *P/B* index for the larvae is 4.6), the mean annual *P/B* ratio for all developmental stages increases to 5.0 (Siegel 1986).

Total production, somatic growth, moult, and egg production

Production of *Nyctiphanes couchii* in the Northeast Atlantic is among the lowest reported for upwelling species (Table 5) (Lindley 1982*a*). Higher values were reported for *N. australis* off Tasmania (Ritz and Hosie 1982). This is substantially lower than the production observed for *N. simplex* off Baja California (Lavaniegos 1995; Gomez-Gutierrez et al. 1996), although large latitudinal variations occur for this species (see Table 5). The average abundance and biomass of *Nyctiphanes capensis* are remarkably high compared with estimates for other euphausiid species. Applying a conservative *P/B* ratio of 4, *Nyctiphanes capensis* could produce more than 10 g dry weight·m^{-2}·$year^{-1}$ in the Benguela Current, which is an enormous amount of food for potential predators (Barange and Stuart 1991). Similar high values were recorded for *E. pacifica* off Japan (Iguchi and Ikeda 1999) and *E. lucens* from the Benguela upwelling system.

When production of exuviae and eggs is considered, the total production for *E. pacifica* would double to approximately 15 g dry weight·m^{-2}·$year^{-1}$ (Iguchi and Ikeda 1999). For *E. lucens*, it would at least double and range between 14 and 47 g dry weight·m^{-2}·$year^{-1}$ (Stuart and Pillar 1988). This is among the highest recorded to date. This remarkable productivity is likely because of the abundant food supply in the area, which Stuart and Pillar (1988) supposed arises from the interaction of coastal upwelling, strong offshore fronts and advective processes together with multiple breeding events and relatively warm constant-temperature conditions. Similarly, high productivity levels are observed in other upwelling areas, e.g., off British Columbia for *T. spinifera* and *E. pacifica* (Table 5). The similarly high production due to growth in polar *E. superba* (12 g dry weight·m^{-2}·$year^{-1}$; Siegel 1986) can be explained as a result of the high population biomass of this species.

Data collected in oceanic and shelf areas as well as in different years indicate that net production rates may be subject to interannual or geographical variation (Lindley 1980), and since biomass fluctuates simultaneously, *P/B* ratios vary accordingly. The interannual variability in net production for *M. norvegica* was highest in Norwegian waters, reaching a factor of 7- to 13.5-fold between two years, while productivity in the North Sea and in the oceanic North Atlantic was more stable (a factor of 2–7.7). Since biomass fluctuated in the same direction as production, the interannual variability in the *P/B* indices was less pronounced and ranged between a factor of 1.1 and 4. The high interregional differences can be explained by the very high productivity in Norwegian waters in one year, while a relatively constant net production could be observed across the rest of the North Atlantic.

Production of the genus *Nyctiphanes*, a genus distributed worldwide in upwelling regions, shows seasonal as well as interannual variability. Interannual variability in production was observed for *N. couchii* off the Irish coast; in one year, net production was relatively low and in the next year was more variable but in general reached a much higher level (see Table 5; Lindley 1982*a*). *Nyctiphanes simplex* off Baja California has a high annual productivity, but production undergoes strong seasonal changes coupled with regional oceanographic conditions. Production (and biomass) are highest in spring and early summer when phytoplankton and zooplankton biomass is at a maximum. Euphausiid production de-

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creases after the end of the upwelling season and with the abrupt increase in temperature. Production is minimal in November when the water column becomes stratified and phytoplankton and zooplankton decrease. There are, however, latitudinal differences in the timing and intensity of production, with lower production to the south and a latitudinal delay of maximum production to the north (Gomez-Gutierrez et al. 1996).

Tanasichuk (1998*a*) identified several aspects of production in *T. spinifera* off British Columbia (Table 5). Firstly, larval and adult production varies interannually; it was high in 1992 and 1993 for both life stages and was low in 1994 and 1995 for both stages. Secondly, *P/B* ratios are high in larvae and lower but more stable in adults. Thirdly, net production of larvae can exceed production of adults by a factor of 6 during the same year.

Although interannual variability in *E. pacifica* is as high as in *T. spinifera*, very high production rates occurred in different years for the two species. Tanasichuk (1998*b*) separated *E. pacifica* larval from adult production and observed 8-fold interannual changes in larvae productivity, while adult production may vary by a factor of 2–3 over several years. The conclusion is that the highest variability occurs in larval abundance and consequently larval productivity, which in general drives the overall *P/B* ratio and the productivity of the population. However, high larval production does not guarantee high adult production because subadult mortality may be high.

For some species, moulting forms a significant contribution of organic material. The upwelling species *E. lucens* utilizes 39–56% of the total dry weight production for somatic growth (P_g), 39–59% of the annual production is due to moulting (P_e), and only 3–6% is used for reproductive effort (P_r) (Stuart and Pillar 1988). Production of exuviae of *N. australis* in temperate waters off Tasmania is about 33% on average, whereas egg production contributes only about 3% to the total production (Hosie and Ritz 1983). *Nyctiphanes simplex* in subtropical waters shows similar values, 23.4% for exuviae and <2% for egg production (Lavaniegos 1995). In *E. superba*, exuviae production is comparatively less, about 13.8% of the total dry weight production are moults (Siegel 1986), and thus has little effect on the overall net production. This is most likely due to the prolonged generation times and intermoult periods in polar species.

It has to be considered that the ratio of production by growth can be strongly influenced by the actual number of larvae in the population because of their higher growth rate than larger specimens. According to Tanasichuk (1998*b*), *E. pacifica* larval moult production can account for 15–20% of the total larval production, while adult moult production was as high as 40–58% of the total adult production. In this case, total productivity was similar for the adult and larval stock. The estimated production of moults from these species is 6–7 times the mean euphausiid biomass.

From the above figures, egg production does not seem to play a major role in comparison with total productivity. However, Stuart and Pillar (1988) pointed out that this may be a misinterpretation due to the dry weight measurement in productivity. The loss of body carbon due to egg production can be as high as 234% of the body carbon in females that undergo several spawning events during a 1-year life cycle (Ross et al. 1982). Replacing dry weight production for growth, exuviae, and eggs by carbon production, then the portion of exuviae production of *E. lucens* would be reduced to P_e = 6%, while the production for reproductive effort would increase to P_r = 60% (Stuart and Pillar 1988). This approach would degrade the importance of exuviae production and heighten the significance of reproductive effort.

The carbon production method was also applied to *E. pacifica* off Japan and resulted in 63% growth production, 18% moult production, and 19% egg production. The production for growth resembles more the data from other euphausiid species, but the investment of carbon in egg production is again higher than the dry weight method would suggest, although it does not come close to that found for *E. lucens* with a multibreeding behaviour during a 1-year life cycle (Iguchi and Ikeda 1999).

Iguchi and Ikeda (1999) went one step further and determined assimilation, which is the sum of production and metabolism including energetic costs for vertical migration and basic metabolism. Under these considerations, 48% of the carbon budget goes into basic metabolism and 23% into vertical migration activities. This leaves only 29% for the entire production, of which somatic growth requires the most (P_g = 18%).

It is a well-established fact that secondary production is limited by the amount of available primary production; however, consumption efficiency may vary substantially between populations or species. Few results are available for euphausiid species; nevertheless, they are quite interesting. *Thysanoessa inermis* and *T. raschii* production rates were estimated to be 2–124 mg $C \cdot m^{-2} \cdot day^{-1}$ and ingestion during the spring bloom of phytoplankton to be 6–193 mg $C \cdot m^{-2} \cdot day^{-1}$. This amounts to very little of the daily primary production, only 1–6% (Smith 1991). In the North Sea, similar low rates were described for the potential use of spring blooms by euphausiids (Lindley and Williams 1980). These authors determined total net production of *T. inermis* in the northern North Sea and estimated the necessary carbon ingestion by this population to support this production. Interestingly, the total carbon consumed was only 1.5% of the daily primary production measured over the same survey period. This surprisingly demonstrates the little effect of euphausiid grazing on control and depletion of primary production. Obviously, these northern areas are highly productive and the euphausiids do not exhaust the capacity of their habitat. It would be interesting to see similar investigations on euphausiids from oceanic warmwater or Antarctic regions with a much lower primary productivity.

Recruitment

Recruitment has hardly been estimated in euphausiid species until recently when it was introduced for the commercially exploited species *E superba* (de la Mare 1994*a*, 1994*b*). For some other species, we only find preliminary descriptive comments on the success of single or few cohorts.

Recruitment of *E. pacifica* in Californian waters already occurs after about 30 days, when the larvae enter the juvenile phase. At least four generations are generally reported each year. Due to the short life span and few cohorts, the

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maximum stock size of this species is reached immediately after successful recruitment of a single cohort. In most years, the highest recruitment is observed for the spring and summer cohorts, the while autumn and winter cohorts show low recruitment (Brinton 1976). In general, there is no spawning stock – recruitment relationship. However, a Ricker-type stock – recruitment relationship was found for *E. pacifica* off British Columbia (Tanasichuk 1998*b*), showing a negative relationship between high spawning stock size and larvae abundance, while the population was able to produce an exceptionally high larval recruitment even at a very low level of spawning stock size. This may point to the effects of cannibalism at higher spawning stock densities.

While up to four or more *E. pacifica* cohorts recruit off California every year, there is only one large pulse of larvae recruiting in spring off the coast of Washington. There is apparently no recruitment during winter, as is the case off California. Low temperatures cannot be responsible because reproduction of this species occurs in the northwestern Pacific at even lower temperatures. Another possibility could be that survival of overwintering adult *E. pacifica* is low due to predation in spring and summer and only few 1+ adults remain to spawn in late summer. At the same time, only few age-0 animals are able to mature fast enough to spawn during their first year of life (Ross et al. 1982).

In the protected fjords of British Columbia, recruitment occurs after around 47 days, which is later than off California (Tanasichuk 1998*b*). In contrast with Washington waters, this author sees evidence for four to six cohorts recruiting every year with generally two little successful spawning events in winter. He believes that good recruitment is not directly triggered by warm water (El Niño events) but is caused by strong upwelling in the area preceding the warmwater events and that the high productivity rates are due to a very strong cohort born earlier and passing through the population.

This idea would be in conformity with Smiles and Pearcy (1971), who argued that off Oregon and California, spawning and recruitment success strongly depends on upwelling conditions and is related to primary production and possibly to the lack of large seasonal temperature fluctuations. The onset of upwelling would be the critical period for larvae to get enough (quantity) and possibly also the necessary type (quality) of phytoplankton to attain a better growth rate. After Daly (1991), small changes in growth rates of krill larvae may cause high fluctuations in recruitment. Most notably, the eggs and F1 and F2 stages are responsible for peak recruitment success elasticity (Rumsey and Franks 1999). Obviously, a combination of predation, food limitation, and possibly cannibalism for eggs and larvae restricts the period of successful recruitment for *E. pacifica*.

Elasticity is defined by a proportional change in vital parameters (and is therefore dimensionless) and thus may reflect possible developmental variability in egg and single larval stages. This means that stages with the highest specific mortality and prolonged stage duration affected total larval survival the most; in the present example, eggs and F1 and F2 stages have the highest stage-specific mortality rate and consequently determine recruitment success (Rumsey and Franks 1999).

The large effects of eggs on later recruitment success indicate that female nutrition at the beginning of the spawning season is of great importance in determining egg viability as well as subsequent nonfeeding naupliar stages. Environmental conditions in which eggs are released will certainly play another key role in the survivorship of the hatching larvae. Poor feeding conditions due to bad timing of spawning will not favour survivorship, even if eggs and nauplii were well conditioned. However, again, the length and timing of the spawning season depend, at least in part, on female nutrition. Surprisingly, the C1 stage showed little impact on the recruitment success, although this stage marks a major physiologic transition from nonfeeding to feeding larval stages. Rumsey and Franks (1999) suspected that they probably underestimated the mortality rates of C1 because their projections were based on experimental data under ad libitum feeding conditions. Under less favourable conditions in the field, the C1 stage could be of greater influence on recruitment success. It is thought that the higher variability in F1 and F2 stage duration is responsible for the higher mortality rate and finally for the overall recruitment success. Reasons for this are presumably the development of pleopods and gills together with higher oxygen consumption and growth rates. These higher energy requirements represent an additional burden on the carrying capacity of the respective developmental stages in a variable environment

In the Barents Sea, a long-term 12- to 14-year periodicity of overall krill density was reported to be possibly coupled with a high-frequency 2- to 3-year variation in krill recruitment (Drobysheva 1994). This recruitment was defined as the transition from the larval to the juvenile 0+ age group. The changes in recruitment were explained by influences of water temperature on the youngest age group, so that the effects can be seen with a time lag of 1 year (Drobysheva 1987). This would allow predictions about possible recruitment success of *T. inermis* stocks. According to Drobysheva (1987), the *T. raschii* stock shows a similar cycle, but she argued that for this more inshore species, the cycle results from underexploitation of the resource by its major fish predators during cold years.

Recruitment of *E. superba* was first defined as the proportion of recruits known as the R_1 rate, which is the ratio of numbers in age-class 1 to the numbers in age-class 1 and all age-classes above (de la Mare 1994*a*). This procedure can also be applied to age-class 2. Since krill distribution is extremely patchy, neither stock density estimates nor density estimates for each length-class of standardized length–frequency distributions show a Gaussian distribution. The underlying statistics of these distributions were analysed and a new approach was developed by de la Mare (1994*b*) to create density at length (instead of length–frequency) data from scientific surveys as a basis for recruitment estimates. However, some of the survey results on R_1 and R_2 given by de la Mare (1994*b*) for the Atlantic sector are not representative because these calculations did not consider the incomplete survey coverage of the stock and its underlying geographical nonrandom distribution pattern of different age groups (Siegel et al. 1997).

One disadvantage of the proportion of recruits is that a high proportionate value can have different meanings when stock density is either very high or very low. By standardiz-

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ing the number of recruits to a given density (number of recruits per 1000 m^3), this new index was defined as absolute recruitment of 1-year-olds (RI_1; Siegel et al. 1998).

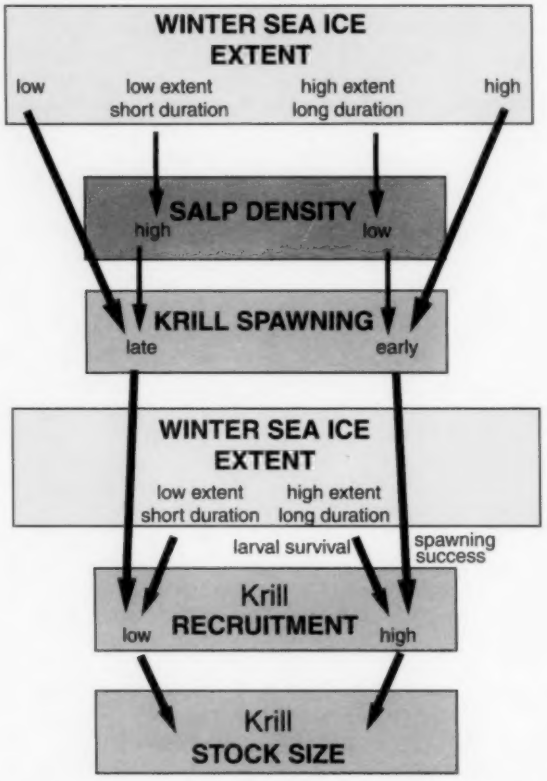
Another disadvantage of the proportional index is that it does not necessarily provide an indicator of reproductive success because it does not refer to the reproductive stock of the previous year but to the year of the survey when recruitment takes place and the assumption of a closed krill population considered to be in equilibrium is far from being realistic. In reality, large variations in stock and spawning stock size are quite obvious from krill net survey estimates, although these changes in abundance usually occur gradually over several years and not from one year to the next (Siegel et al. 1997, 1998).

However, some conclusions can still be drawn from the presently defined recruitment indices. The longest time series exists for the Antarctic Peninsula region where recruitment peaks were observed for the year-classes 1980–1981, 1981–1982, 1987–1988, and 1994–1995. It is also evident that most values from scientific surveys since the mid-1980s show generally poor recruitment results, which might explain the low stock size in the 1990s (Siegel et al. 1997, 1998). No stock–recruitment relationship could be found for Antarctic krill (Siegel and Loeb 1995), and the very strong 1994–1995 year-class demonstrated that even at a low spawning stock level, extraordinarily strong cohorts could be produced.

It is obvious that the results differ substantially between years and regions. Various parameters had been tested to find possible links between krill recruitment and the biological and physical environment. The most promising variable for explaining the high variability in krill recruitment was sea ice (Siegel and Loeb 1995), especially the spatial extent and duration of winter sea ice cover. Since sea ice seems to work on different levels of krill population dynamics, a conceptual model was developed by Siegel and Loeb (1995) based on significant correlations of various parameters (Fig. 1).

Long sea ice cover and a large spatial extent during winter are favourable for an early onset of the spawning season, probably due to the ice-algae resource available to krill during late winter to early spring. Protection from predation may be another reason for a higher survival rate. Salps as opportunistic short-lived animals may compete with *E. superba* for phytoplankton and may have an adverse effect on krill recruitment (Loeb et al. 1997). As a consequence of favourable sea ice conditions, early reproduction leads to a successful spawning event in summer. Siegel and Loeb (1995) hypothesized that the ice-algae resource in late winter and early spring might be essential for adult krill to gain enough energy for an early onset of the reproduction process, which would favour the larval survivorship. Larvae that hatch early in summer show a high rate of survival during the feeding and growth season and are well conditioned before their first winter. This is important, since Torres et al. (1994) suggested that the impact of the winter season is most severe in the smaller size-classes. The approach on elasticity and sensitivity of larval stages on recruitment success of *E. pacifica* (Rumsey and Franks 1999) strongly supports this idea. Not only does recruitment depend on the supply of well-conditioned eggs from spawning females and the subsequent survival of larvae, but timing and the length of the spawning season also depend at least partly on female nutrition (Rumsey and Franks 1999).

Fig. 1. Hypothesis on the relationships between krill recruitment success and environmental (sea ice condition) and biological factors (salp abundance, spawning timing). Modified after Siegel and Loeb (1995).



Geographical differences in Antarctic krill recruitment are quite obvious from Table 6. As an example, the year-classes 1980–1981 and 1985–1986 were highly successful in the Atlantic sector, while recruitment in the Indian Ocean was a failure during the same years. On the other hand, the year-class 1988–1989 experienced high recruitment in the Indian Ocean, but it was low in the Atlantic. This is no surprise because Stammerjohn and Smith (1996) demonstrated that individual regions of the Southern Ocean show significant interannual variability in ice coverage with no coherence between the Antarctic Peninsula region and the Indian Ocean sector. Due to these differences in the periodicity of ice conditions for different subregions of the Antarctic Ocean, krill recruitment indices have to be estimated and interpreted separately.

These results lead to the conclusion that recruitment success and finally stock size of *E. superba* as a result of interannual variation in year-class success appear to be generated by environmental effects (sea ice effect on larval survival) and not by changes in biological characteristics of the euphausiid. Indeed, spawning timing does influence reproductive success and thus cohort strength for many euphausiid species including *E. superba* and *E. pacifica*, but the onset of the spawning

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Table 6. Recruitment of *E. superba*.

	Proportional recruitment at age 1 (R_1) or 2 (R_2) years						
	Indian Ocean (de la Mare 1994*b*)		Antarctic Peninsula (Siegel et al. 1998)		R_2 (Kawaguchi et al. 1997)		
Year	R_1	R_2	R_1	R_2	Livingston Island	Elephant Island	RI_1 (Antarctic Peninisula) (N·1000 m^{-3})
1975–1976				0.144			
1976–1977			0.048				16.71
1977–1978							
1978–1979		0.096		0.069	0.336	0.451	
1979–1980	0.167	0.561	0.559		0.000	0.086	90.21
1980–1981	0.001		0.757		0.462		245.93
1981–1982		0.557	0.470	0.663	0.585	0.427	130.05
1982–1983	0.016	0.431	0.030	0.0001	0.156	0.142	4.59
1983–1984	0.528		0.0001	0.214	0.147	0.072	0.01
1984–1985		0.231	0.175		0.191	0.165	
1985–1986	0.025			0.633	0.316	0.334	
1986–1987			0.156	0.291	0.194	0.360	4.31
1987–1988			0.651	0.275	0.000	0.000	51.98
1988–1989		0.556	0.057	0.063	0.000	0.000	0.88
1989–1990	0.314		0.099	0.345		0.083	0.64
1990–1991		0.02	0.375	0.587	0.574	0.129	7.45
1991–1992	0.064		0.000	0.012	0.719	0.169	0.00
1992–1993			0.068	0.029	0.000	0.000	2.24
1993–1994			0.046	0.125	0.058	0.000	3.37
1994–1995			0.622	0.837			74.62
1995–1996			0.198	0.384			42.07
1996–1997			0.120	0.000			3.06
1997–1998			0.000				0.00

Note: Year is when the year-class was born.

event again is determined by sea ice or upwelling conditions via the related food/prey availability.

In light of possible long-term changes like global warming or ozone depletion, effects might be expected at the individual or population level of euphausiid species. For waters off southern California, Roemmich and McGowan (1995) reported a warming of surface water and a reduced upward displacement of the thermocline. With a shallower source of upwelled water, fewer inorganic nutrients are responsible for a reduced biological production. Since the early 1950s, biomass of macrozooplankton including the dominant euphausiids has decreased by 80%.

Observed increasing air temperature in the Southern Ocean will affect sea surface temperature and sea ice conditions. Consequently, this will affect krill recruitment and krill stock size in the long term. Increased ultraviolet-B radiation might be another variable that might damage near-surface krill concentrations (Jarman et al. 1999; Naganobu et al. 1999; Newman et al. 1999) and increase mortality rates, which again would reduce recruitment success and overall krill biomass. The current low recruitment rates for *E. superba* over many years have to be regarded with some concern. The krill stocks and the population dynamic parameters have to be taken as warning signals and to be monitored carefully to gain a better understanding of the development of these stocks as key elements of marine ecosystems. One crucial question to answer is do our observations represent just high interannual variability in the past two decades or might it turn out as a starting point of a downward trend? In other words, species like *E. superba* are obviously sensitive to changes in their habitat over a scale of months to several years. They seem to have adapted not only to an average situation but also to some degree of variation in the system. However, whether these species will be able to cope with increasing variability (increasing temperature, decreasing ice extent, increasing ultraviolet-B radiation) is an open question. If this new dimension in variability of external factors exceeds the potential of krill to adapt, then krill stocks and consequently dependent species will not be able to sustain their populations.

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PERSPECTIVES

Krill (Euphausiacea) demography and variability in abundance and distribution

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Abstract: Among euphausiids, there are many species that are represented by enormous numbers of individuals and are of considerable importance to various ecosystems, as well as to human exploitation. Considerable progress has been made regarding quantitative aspects of krill biology. This detailed knowledge about krill population parameters is necessary to answer questions about the importance of euphausiids to energy flow through certain ecosystems. This information also helps in assessing the importance of seasonal or long-term climate effects on variation in euphausiid populations because variability is not simply noise. Hypotheses have been developed as to how large seasonal or latitudinal environmental changes affect species survival strategies in poor conditions and maintenance of a stable population level. This paper discusses aspects of the spatial distribution with regard to seasonal and interannual changes, developments to define genetically distinct populations, and results of long-term variability in krill abundance and biomass for various species in different geographical locations.

Résumé : Parmi les euphausiacés se trouvent de nombreuses espèces représentées par des quantités énormes d'individus et jouant un rôle considérable dans divers écosystèmes ainsi que pour l'exploitation humaine. Des progrès remarquables ont été réalisés sur les aspects quantitatifs de la biologie du krill. Ces connaissances détaillées des paramètres démographiques du krill sont nécessaires pour répondre aux questions sur l'importance des euphausiacés pour le flux d'énergie dans certains écosystèmes. Cette information sert aussi à estimer l'importance des effets climatiques saisonniers ou à long terme sur la variation des populations d'euphausiacés, car la variabilité ne doit pas être considérée simplement comme un bruit. Diverses hypothèses ont été formulées pour expliquer en quoi les grands changements écologiques au niveau des saisons ou de la latitude affectent les stratégies de survie des espèces dans des conditions défavorables et le maintien d'un niveau de population stable. Cette étude analyse : (1) certains aspects de la distribution spatiale par rapport aux changements saisonniers et interannuels; (2) les progrès réalisés pour définir des populations génétiquement distinctes; (3) les résultats de la variabilité à long terme de l'abondance et de la biomasse du krill pour diverses espèces occupant différentes régions géographiques.

[Traduit par la Rédaction]

Introduction

Euphausiid species are widespread in the world's oceans and range from tropical to high polar regions. Among these are many species thst are represented by enormous numbers of individuals. As a result, these species are of considerable importance to various ecosystems but also to human exploitation. However, very few accounts in the literature attempt to review and answer essential questions about the importance of euphausiids in energy flows through certain ecosystems. Only recently was it realized that seasonal or long-term environmental effects are important for the variability in euphausiid populations. Even simple descriptive aspects of the krill life cycle such as distribution patterns turned out to vary on different time scales. Even higher variability was observed in quantitative population parameters of some species. Topics of this sort are not only of theoretical interest, but also, potential climate changes and human fishing activities may influence the krill stocks in the future. Basic quantitative data on abundance and density and the knowledge about the distribution and geographical boundaries of a population (genetic structure) are essential to gain an understanding of population size. If a population were spread uniformly over its whole habitat, a single value for population density would apply throughout. But mostly, the organisms are concentrated in certain parts for whatever reason, resulting in uneven dispersion. Truly, a more spatial coverage of a large proportion of the population and regular investigations are highly desirable for understanding population stability or variability. Monitoring these characteristics over time would enable us to finally manage the population and its dynamics.

Despite their presence and importance in most of the world's oceans, Euphausiacea (krill) have not been studied to the same extent in different parts of the world. There are excellent monographs in the literature on some species like *Euphausia superba* or *Euphausia pacifica* (e.g., Brinton 1976; Miller

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and Hampton 1989). However, it seems important that these summaries are updated with more recent data and conclusions. Quantitative research is still scarce on tropical oceanic or mesopelagic krill species, and valuable information is widely spread in the literature but needs to be considered and discussed in a more general context. It will not be possible for this perspective to cover all species for which relevant data are available. Due to the large amount of new information, the present contribution will focus on species for which data have been collected over a longer time period so that we can gain some understanding of variability or species plasticity during their life cycle.

Krill population characteristics

To understand the biology of a population, we need a sound knowledge of the biology of the individuals comprising it. Primarily, we should be aware of features such as the distribution, abundance, size, life cycle, and behaviour of the organisms concerned. Furthermore, for various, often compelling, practical reasons, we need to learn something of their genetic makeup and the genetic pattern of the population as a whole.

Identification of populations

Panmixis across zooplankton species is not usual, although even on a large scale, physical or biological phenomena are rarely preventing random interbreeding. The question is whether the relative similarity of the physical oceanic environment is reflected in similar values for the heterogeneity. In other words, is there a chance for demographic isolation and the establishment of genetically different populations in a species habitat under conditions of large-scale advection, active migration, and a relatively long life span of the species, which should at least theoretically allow for interbreeding from time to time? The answer to the question is of some importance because the genotype and the environment, as well as the interaction between these two, clearly reflect the life history of the species and the ability to adapt to a changing environment. Furthermore, from a more practical point of view, the assessment and management of euphausiid stocks require information on subunits of the species before dealing in detail with the specific structure and dynamics of such populations. Several examples have been investigated in the past with sometimes conflicting results.

Euphausia krohnii and *Nematoscelis megalops* in the northeast Atlantic show significant heterogeneity of allozyme frequency in electrophoretic analyses, indicating the existence of heterogeneous local populations (Bucklin 1986; Bucklin and Wiebe 1986). There was no spatial or temporal pattern associated with the genetic distance measure, and despite the small sample size, sampling error could be considered minimal, but the authors did not excluding the possibilities that sea surface temperature differences or reproductive events may cause changes in the genetic structure of the species.

According to Brinton (1976), *E. pacifica* shows multiple centres of recruitment and persistent, geographically stable aggregations along the coast of California. Genetic studies for allozymic variability resulted in significant genetic differentiation of samples over rather short geographical distances. Bucklin (1986) argued that these results indicate the existence of local *E. pacifica* populations distributed as a two-dimensional array with isotropic migration between adjacent populations and further concluded that genetic homogeneity of zooplankton populations over even short distances cannot be assumed.

On the other hand, the total average heterozygosity for *Meganyctiphanes norvegica* and *Thysanoessa raschii* is very low. This low genetic variation may reflect the similarity of the physical environment for the two species (Fevolden 1982). Sundt and Fevolden (1996) studied *M. norvegica* from Spitsbergen, Greenland, Iceland, and Norway and observed a high degree of homogeneity when applying isoenzyme analyses. They concluded that this northern krill represents a single panmictic population in the Northeast Atlantic. Despite regional differences in growth of the species, these authors argued that differences in growth are not genetically driven but rather ecologically driven. In their opinion, the genetic differentiation would be a long process after a reproductive isolation simply because of the huge population size. It is probable that a complete demographic isolation over long periods is required to produce detectable differences in allele frequencies at neutral loci.

Comparison of *M. norvegica* samples from the Northwest Atlantic and Norwegian waters showed significant differences in haplotype frequencies for cytochrome *b* and the cytochrome oxidase/CYB sequence. This indicates a highly restricted gene flow across the North Atlantic and the establishment of distinct populations. However, the samples from various sites within the Northwest Atlantic did not reveal significant differences. It can therefore be concluded that gene flow of *M. norvegica* along the North American east coast is sufficient to prevent the formation of distinctive geographical populations. From their study, Bucklin et al. (1997) concluded that a large sample size is required on an appropriate temporal and spatial scale when investigating resolution of population genetic structure of euphausiids at spatial scales smaller than ocean basins.

With these comments in mind, one has to regard the results recently described from a genetic study on *M. norvegica* (based on a single-strand conformation polymorphism analysis), which covered samples from several locations in the Northeast Atlantic and the Mediterranean Sea. The results partly confirm the homogeneity of the Northeast Atlantic found by Sundt and Fevolden (1996) but partly contradict their conclusion of panmixis for *M. norvegica* because significant differences were detected among Northeast Atlantic, Cadiz Bay (outside the Mediterranean), and Ligurian Sea samples (inside the Mediterranean). These were interpreted as three distinct genetic pools. A sample taken east of Gibraltar was genetically intermediate between Northeast Atlantic and Ligurian Sea samples. (Zane et al. 2000). It was argued that the genetic segregation is not associated with the Gibraltar Strait but with a frontal system east of the Strait that separates the Cadiz and eastern Gibraltar breeding units.

Mackintosh (1972) first introduced the term "stock" for *E. superba* because of high krill density areas in the Antarctic Ocean, but he himself never argued that these stocks are self-maintaining units as was later often interpreted by other authors (Bellingshausen stock, Weddell stock, Kerguelen–Gaussberg stock). The results of Hosie (1991) on the drift and advection of krill larvae from the Prydz Bay area demon-

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strated that this highly variable and dynamic process does not support the idea of a self-maintaining Kerguelen–Gaussberg stock. On the other hand, Makarov and Maslennikov (1981) studied furcilia developmental pathways of *E. superba* and found differences north and south of the Weddell–Scotia Confluence zone, which they interpreted as characteristics of different populations.

Siegel (1986) used morphometric measurements of *E. superba* from the Antarctic Peninsula, the northern Weddell Sea, and the Indian Ocean to identify separate stocks. However, statistical analyses did not result in significant differences between any geographical regions.

Studies of allozymic variation in zooplankton populations have demonstrated that plankton species are highly genetically variable. High variability provides numerous allozymic variants for potential indicators of genetic divergence (Bucklin 1986). During the past 20 years, alloenzyme electrophoresis has been used in determining the level of genetic differentiation in intraspecific krill populations.

Euphausia superba exhibits no differences in allozymic frequency among samples from areas almost around the entire Antarctic and thus no apparent genetic structuring into populations (Fevolden 1988; Fevolden and Schneppenheim 1988, 1989). According to these results, *E. superba* shows genetic homogeneity within different regions and obviously does not form closed populations. However, exchange rates between different regions are unknown, but even quite low rates could account for the observed level of genetic homogeneity. Occasional intersample heterogeneity and deviation from the Hardy–Weinberg equilibrium are interpreted as environmentally influenced selection rather than isolated populations (Fevolden 1988). Investigations on other Antarctic species, *Euphausia crystallorophias*, also demonstrated the lack of genetic heterogeneity (Kühl and Schneppenheim 1986).

Molecular evidence for genetic subdivision of *E. superba* populations was first given by Zane et al. (1998). This mitochondrial DNA sequence analysis of krill from the Bellingshausen, Weddell, and Ross seas as well as from South Georgia in the South Atlantic resulted in a significant difference between population samples from South Georgia and the Weddell Sea. No significant differences were observed between the other regions, despite the larger geographical distance between them. Considering the present thinking about large-scale oceanographic connections, this result is less surprising than it might appear at first instance. The Bellingshausen Sea seems to serve as the upstream area via the West Wind Drift along the peninsula towards South Georgia, and the Ross Sea is linked to the Bellingshausen Sea via the East Wind Drift. On the other hand, South Georgia probably comes under the influence of the Weddell Sea only every other year.

Interannual variability is also a reason for Zane et al. (1998) not to exclude the possibility of temporal rather than geographical genetic differentiation. In their opinion, there are reasons to believe that genetic drift associated with a high variability in reproductive success could play a role in differentiating krill populations. Future studies have to verify whether such genetic differentiation is geographically and temporally stable.

Zane et al. (1998) took their genetic diversity studies one step beyond the identification of distinct krill populations. They investigated mutation drift equilibrium and the neutrality hypothesis for *E. superba* at the species and the population level. The neutral theory of molecular evolution states that high levels of genetic variability should be related either to high mutation rates or to temporally stable population size (Kimura 1983). From the observed distribution of mitotypes in *E. superba* and the significant departure from the equilibrium hypothesis, the authors concluded that in the past, the Antarctic krill population has undergone a major expansion or a reduction followed by an expansion. These dramatic fluctuations in population size may have occurred over a period ranging between 16 000 and 324 000 years ago, from which the present population of Antarctic krill is still recovering.

Krill distribution

Previously, I presented the importance of distribution patterns for the development of distinct populations. Many populations fluctuate considerably in abundance and spatial distribution characteristics, some slowly, some rapidly, with varying amplitude and frequency.

One example of how krill distribution may be affected by variable current patterns is the distribution pattern seen in *E. pacifica* stocks at the fringes of their range, especially in the California Current. Similarly, the ranges of *Thysanoessa* species off northern Norway and in the Barents Sea vary both seasonally and interannually, due likely to intensity variations in the North Atlantic Current. The Antarctic krill *E. superba* has a distribution range along the Antarctic Peninsula that exhibits regular seasonal and interannual fluctuations and rapid unpredictable changes near its northern limits.

Thysanoessa inermis and *T. raschii* are especially abundant in the Barents, Beaufort, and Chukchi seas. In the Beaufort and Chukchi seas, stocks receive additions from the Bering Sea where *T. inermis* lives along the shelf edge and *T. raschii* is present in shallow shelf waters. Earlier, the East Siberian and Laptev seas, between the Barents and Chukchi seas, were thought not to sustain these species and neither was the Canadian Archipelago north of Queen Elizabeth Islands (Geiger et al. 1968). Thus, it was not clear if these species had a circumpolar distribution or if the Atlantic and Pacific populations were completely separated. However, according to Drobysheva (1994), both species occur at least sporadically as adults in the Kara and Laptev seas, spreading mainly from west to east and thereby probably facilitating gene flow between stocks found in the Pacific and Atlantic oceans. Unfortunately, no studies based on molecular genetics have hitherto been presented for these species from different parts of their large distribution range.

In the Barents Sea, yearly shifts in the distribution of *Thysanoessa* species and *M. norvegica* have been attributed to invasions during unusually warm years (Dalpadado and Skjoldal 1991; Drobysheva 1994). However, no immediate correlation is obvious between long-term temperature anomalies and euphausiid abundance (Fig. 1). Undoubtedly, years with stronger drift of the North Atlantic Current carry krill into northern waters, but it is unlikely that increasing temperature is the proximate cause of their occurrence at these high latitudes.

The proximate mechanisms that affect and determine distribution and density of krill are still under discussion in

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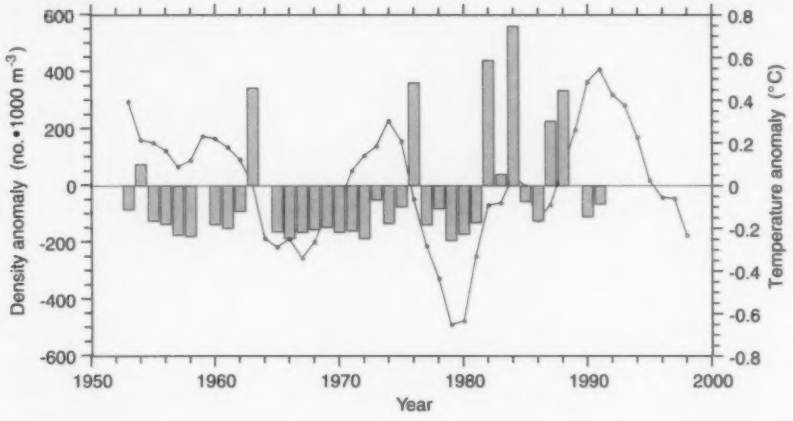
Fig. 1. *Thysanoessa inermis* numerical density anomaly (bars) and sea surface temperature anomaly (line) in the Barents Sea. Data source: Drobysheva (1987, 1994).



most cases. To illustrate these points, one should consider the influence of frontal systems on the distribution and abundance of krill species, which was clearly described for the Kuroshio–Oyashio Front off Japan by Nishikawa et al. (1995). According to this study, *E. pacifica* occurred abundantly (5406 individuals·1000 m^{-3}) on the cold side of the front in productive Oyashio water, while the species disappeared completely on the warm, less productive Kuroshio side of the front. In a warmwater intrusion in the mixing zone between these water bodies, abundance was low (372 individuals·1000 m^{-3}). In this case, krill seemed to prefer high productivity instead of warmer temperatures. This apparent preference of euphausiids for different current systems with differences in productivity may also explain the observation by Taki et al. (1993). These authors reported that catch per unit effort values of *E. pacifica* in Japanese waters were high in years with temperatures below average and low in years when temperatures were above average. One cannot exclude the possibility that this phenomenon may be an effect of something other than temperature. It seems just as likely that the correlation with temperature may be an effect of predominance of different currents having different sets of other habitat characteristics (e.g., productivity), which in turn may coincidentally correlate with temperature.

Upwelling periods have some influence on euphausiid species composition, distribution, and abundance. Strong upwelling effects along the western coast of the United States seem to favour the dominance of euphausiids in the area compared with other zooplankton species. In contrast, weak upwelling seems to generate higher trophic diversity. In years strongly affected by the El Niño phenomenon, upwelling is weaker, which favours higher species diversity as a northward shift occurs in the Subarctic Boundary from California to British Columbia. This shift is accompanied by intrusion of tropical euphausiid species. In years with weak El Niño effects, like 1986–1987, these tropical species are comparatively rare and little affect the species composition off Baja California (Gomez-Gutierrez et al. 1995). There are, however, observations that, at first glance, seem to contradict this hypothesis. Tanasichuk (1995), for example, reported strong cohorts and consequently high stock abundance of *E. pacifica* in the coastal waters of British Columbia during the 1992–1993 El Niño Southern Oscillation (ENSO). However, the author did not relate the high stock biomass to the warm water ENSO effect but rather to the productive pre-ENSO upwelling conditions. Further relationships complicate the development of the stock size. After the end of the ENSO period, primary productivity should be expected to increase again, but in this case, euphausiid stock biomass declined considerably and Tanasichuk (1995) attributed this to a severe increase in predation pressure by Pacific hake and chub mackerel.

Another example concerns the inshore species *Nyctiphanes capensis* from the Benguela Current off South Africa, which showed maximum densities during austral summer to autumn when temperatures were peaking and minimum densities during spring when temperatures were low. The shelf-break species *Euphausia hanseni* shows a similar seasonal trend. However, despite strong seasonality in the occurrence of upwelling events, distribution patterns of these two species remain relatively constant throughout the year. *Euphausia lucens* shows substantial seasonal fluctuations in monthly abundance and biomass, especially in inshore waters (Stuart and Pillar 1988).

Pillar et al. (1989) and Barange and Stuart (1991) suggested a conceptual model for the maintenance of populations in the Benguela system of *N. capensis*, *E. hanseni*, and *E. lucens*, based on cross-shelf transport of females with spawning females over the outer shelf. Pillar and Stuart (1988) indicated that vertical migration and depth might interact with preferences of early life stages of *E. lucens* for the horizontal and vertical (upwelling) current circulation systems. The general water transport of the Benguela Current surface layer will carry the adult stock northward and offshore, but during intermittent downwelling periods, the transport will be reversed, i.e., onshore. However, deeper countercurrents have a net southerly and onshore component. The vertical migration behaviour of *E. lucens*, according to this one-celled cross-shelf circulation model, thus works to maintain the population in the preferred habitat over the narrow shelf area.

The coastal *N. capensis* and *E. hanseni* found over the shelf break are expected to experience different regimes, which maintains their onshore–offshore segregation. *Nyctiphanes*

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capensis spawn in nearshore waters and carry their developing offspring in brood pouches until they are released as metanauplii. About 90% of the larvae occur below the Ekman layer, while the adults concentrate in this surface layer. This behaviour prevents the eggs and larvae from being transported offshore. Adults and eggs of *E. hanseni* are found in the vicinity of the shelf break, nauplii further offshore, and calyptopis even further, indicating offshore transport of larvae. Onshore displacement occurs when furcilia stages migrate vertically and are entrained in a deeper layer, which is transported onshore and eventually forms an upwelling flow during daytime (Barange and Pillar 1992).

The described one-cell circulation model seems to explain the cross-shelf distribution of *E. lucens* over the southern narrow shelf off South Africa but does not explain the more complicated distribution pattern for the other two species. Therefore, Barange and Pillar (1992, their fig. 9*a*) argued for a two-cell current structure over the much broader shelf areas. This model builds on inshore and shelf break upwelling and sinking inshore of the shelf break front to explain the marked cross-shelf segregation. Furthermore, the northward surface current is probably compensated for by a southward undercurrent, maintaining the vertically migrating postlarval populations in a latitudinally stable distribution pattern.

The above results and hypotheses developed for these Benguela Current species are interesting because they may form a conceptual basis for also explaining observed segregation of species and developmental stages in other upwelling regions. Off Baja California, for example, *Nyctiphanes simplex* occurs in high densities in coastal regions during upwelling conditions without offshore displacement by an associated Ekman surface transport (Gomez 1995). The maintenance of the spatial distribution of this stock may also possibly be explained by a combination of hydrological circulation patterns and vertical migration behaviour that is different from the combination used by the Benguela Current species. In this case, however, large specimens of *N. simplex* have been found offshore, while larval stages occur inshore, which is the opposite of the situation found for *N. capensis* in the Benguela Current. The general principles on which the Benguela Current model builds are probably still applicable, but it will be necessary to modify the model and adapt it to local peculiarities of the California Current system.

Spatial separation of species or even developmental stages is not unique to Benguela Current species; it has also been found in Antarctic species (e.g., *E. superba*, *E. crystallorophias*, and *Thysanoessa macrura* (Siegel 1988; Siegel and Harm 1996)). The seasonal changes in distribution patterns of *E. superba* are described in detail below in the "Seasonal variability in krill abundance" section. At this stage, it should be mentioned that the concept of seasonal distribution patterns and abundance of *E. superba* builds on the assumption that immigration and emigration are important processes behind observed patterns of stock distribution and density. Important, in this context, is information on residence times or exchange rates of the observed biomass of the species in the flow-through system of the Antarctic Peninsula to allow estimates of the total effective biomass within specified regions and time frames. The Elephant Island area is one of the most regularly surveyed sites for krill and can serve as a case study. This area receives water from three different sources: from the west out of Drake Passage north of the South Shetland Islands, from the southwest out of the Bransfield Strait, and from the south out of the Weddell Sea.

A water retention time of 18–44 days has been suggested for the Elephant Island area (50–56°W) based on influx and efflux rates calculated from oceanographic data. In addition, direct measurements of flow are available from Japanese satellite-tracked drifter buoy studies (Ichii and Naganobu 1996). These results indicate the existence of complex eddy formation and prolonged water retention on the island shelves in contrast with the oceanic waters north of the Weddell–Scotia Confluence. Krill in the oceanic water masses show the shortest retention times of 25 days. This meandering and eddy-rich system is characterized by prolonged water retention times of up to 48 days.

In the past, it has been suspected that the Weddell–Scotia Confluence is responsible for the main transport of krill across the Scotia Sea. However, Hofmann et al. (1998) showed that the dynamic feature that transports krill across the Scotia Sea is the southern Antarctic Circumpolar Current. They presented a model for krill transport that takes into account the composite flow field produced by combining the surface Ekman drift, large-scale background flow, and the frontal jets. Results show that wind-induced transport was insufficient to move krill more than a few kilometres per month. These results show that wind-induced transport is sufficient to move krill west of the peninsula into the currents associated with the southern Antarctic Circumpolar Current system. This Antarctic Circumpolar Current high-speed current field transports krill to the northeast across the Scotia Sea to South Georgia in 140–160 days. Other experiments showed that in summer, a shorter period of 2 months might also be possible to carry krill across the Scotia Sea (Ichii and Naganobu 1996).

Against this background, it seems reasonable to expect that krill are regularly drifting into the South Georgia area, but in some years, krill occurrence can change rapidly and dramatically in the area due to northerly weather effects displacing the water masses further to the south (Priddle et al. 1988). The high variability in occurrence and abundance of krill in the waters off South Georgia seems explainable by the fact that these waters are at the extremes of the geographical range of *E. superba* rather than in the centre of its distribution. The special situation for krill around South Georgia is also illustrated by the fact that generally successful spawning of *E. superba* has not been observed in these waters, which are close to the Antarctic Convergence.

Krill abundance

A great number of *E. superba* density and biomass values are widely scattered throughout the published literature. Miller and Hampton (1989) provided a summary of Antarctic krill density estimates. Biomass estimates from the Antarctic Peninsula region have been reviewed by Godlewska and Rakusa-Suszczewski (1988) and more recently data from hydroacoustic surveys by Hewitt and Demer (1994) and Brierley et al. (1999*a*). The present account will concentrate on data that have been collected with standardized methods over several years during mesoscale surveys. This choice of scale is based on the fact that the last real large-scale biomass estimate for the Atlantic sector was the international

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Table 1. Biomass and numerical density of euphausiid species from net and acoustic sampling surveys.

Species	Geographic region	Year	Net or acoustic	Weight
E. crystallorophias	Antarctic, Bellingshausen Sea	1994	Net	
E. crystallorophias	Antarctic, Indian Ocean		Net	
E. crystallorophias larvae	Antarctic, Indian Ocean	1985	Net	
E. eximia	Baja California, Mexico	1993	Net	DW*
E. eximia	Baja California, Mexico	1986–1987	Net	
E. frigida larvae	Antarctic, Indian Ocean	1985	Net	
E. hanseni	Benguela Current	Nov. 1982–1983	Net	DW
E. lucens	Benguela Current	1977–1978	Net	DW
E. pacifica	California		Acoustic	
E. pacifica	British Columbia, Canada	1995–1997	Net	DW
E. pacifica	Baja California, Mexico	1993	Net	DW*
E. pacifica	California		Net	WW
E. pacifica	California		Net	WW
E. pacifica	Okhotsk Sea		Net	WW
E. pacifica	Southwestern Japan		Net	WW
E. pacifica	British Columbia, Canada	1991–1995	Net	DW
E. pacifica	British Columbia, Canada	1991–1995	Net	WW
E. pacifica	Baja California, Mexico	1986	Net	
E. pacifica	Baja California, Mexico	1987	Net	
E. pacifica	Japan		Net	
E. pacifica	North Pacific		Net	
E. pacifica	Washington	1985	Net	
E. pacifica larvae	California		Net	
E. pacifica larvae	Oregon		Net	
E. pacifica larvae	Washington	1985–1987	Net	
E. pacifica larvae	British Columbia, Canada	1995–1997	Net	DW
E. pacifica larvae	British Columbia, Canada	1995–1997	Net	WW
E. superba	Antarctic, Atlantic sector	1981	Acoustic	WW
E. superba	Antarctic, southwestern Indian Ocean	1981	Acoustic	WW
E. superba	Antarctic Peninsula		Acoustic	WW
E. superba	Antarctic Peninsula		Acoustic	WW
E. superba	Antarctic, Elephant Island	1990–1997	Acoustic	WW
E. superba	Antarctic, South Orkney Islands		Acoustic	WW
E. superba	Antarctic, South Orkney Islands	1994	Acoustic	WW
E. superba	Antarctic, South Georgia	1992	Acoustic	WW
E. superba	Antarctic, South Georgia	1990–1997	Acoustic	WW
E. superba	Antarctic, South Georgia		Acoustic	WW
E. superba	Antarctic, west Indian Ocean	1996	Acoustic	WW
E. superba	Antarctic, Indian Ocean	1977–1990	Acoustic	WW
E. superba	Antarctic, Bellingshausen Sea	1992–1993	Acoustic	WW
E. superba	Antarctic, Elephant Island	1978–1997	Net	WW
E. superba	Antarctic, north Weddell Sea	1988–1989	Net	WW
E. superba	Antarctic, 60–64°E	1984	Net	WW
E. superba	Antarctic, Bellingshausen Sea	1993–1994	Net	WW
E. superba larvae*	Antarctic, Indian Ocean	1985	Net	
E. triacantha larvae	Antarctic, Indian Ocean	1985	Net	
M. norvegica	Gulf of St. Lawrence	1982	Acoustic	DW
M. norvegica	Gulf of St. Lawrence		Acoustic	WW
M. norvegica	Nova Scotia	Oct. 1990	Acoustic	
M. norvegica	North Atlantic		Net	
M. norvegica	North Atlantic	1994	Net	
N. difficilis	Baja California, Mexico	1993	Net	DW*
N. australis	Tasmania	1989–1991	Net	DW
N. australis	Tasmania		Net	DW
N. australis	Tasmania		Net	

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Mean regional biomass or numerical density				
$g \cdot m^{-2}$	$g \cdot 1000\ m^{-3}$	$No. \cdot m^{-2}$	$No. \cdot 1000\ m^{-3}$	References
	0.12		2.1	Siegel and Harm 1996
			418	Williams et al. 1986
			564	Hosie 1991
0.000–0.184			37	Gomez-Gutierrez and Robinson 1997
			44–74	Gomez-Gutierrez et al. 1995
			74	Hosie 1991
0.091–0.505			188	Barange and Stuart 1991
	9.7–47.3			Stuart and Pillar 1988
			15 000	Pieper 1979
0.521–0.677		88–102		Tanasichuk 1998*b*
0.000–0.089			19	Gomez-Gutierrez and Robinson 1997
	8–22			Brinton 1976
0.2–1.9				Brinton and Reid 1986
	1.2–67.4			Calculated from Gorbatenko 1996
	2.1–78.3		301 – 76 323	Hirakawa et al. 1992
0.678–1.340		101–204		Tanasichuk 1995, 1998*b*
6.685–19.416				Tanasichuk 1995, 1998*b*
			0.2	Gomez-Gutierrez et al. 1995
			0.2	Gomez-Gutierrez et al. 1995
	0.6–77.0			Taki et al. 1996
			500–5000	cf. Nishikawa et al. 1995
			9 700 – 28 000	Bollens et al. 1992
			5 000 – 10 000	Brinton 1976
			220	Smiles and Pearcy 1971
			600 – 25 000	Bollens et al. 1992
0.039–0.195		479–2723		Tanasichuk 1998*b*
0.131–1.137				Tanasichuk 1995, 1998*b*
8.0–64.4				Trathan et al. 1992
2.3				Trathan et al. 1992
8.0–95.0				Lascara et al. 1999
8–138				Ichii et al. 1998
9.6–100.4				Brierley et al. 1999*b*
17.1–26.3				Kasatkina et al. 1996
10.7				Brierley and Watkins 1996
95.5				Goss and Everson 1996
1.87–94.9				Brierley et al. 1997
4.6–94.9				Brierley et al. 1999*a*
7.6				Pauly et al. 2000
17.5–187.7				Pakhomov 1995
19.6–42.6				Murray et al. 1995
0.98–31.2	4.9–170.8	1.1–48.8	6.5–348.3	Siegel et al. 1998*a*
0.03–2.06	0.5–34.3		0.9–62.4	Siegel and Harm 1996
3.1	62			Aseev et al. 1988
0.03–0.30	0.15–1.52		0.2–2.7	Siegel and Harm 1996
			97*	Hosie 1991
			6	Hosie 1991
			1–32	Simard et al. 1986
2.3–315				Sameoto 1980
		290		Cochrane et al. 1994
			23–976	Lindley 1982
		4.3		Dalpadado et al. 1998
0.004–0.281			59	Gomez-Gutierrez and Robinson 1997
	0.04–1.53		38–1279	Young et al. 1993
	5.39			Ritz and Hosie 1982
			5000	Blackburn 1980

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Table 1 (*concluded*).

Species	Geographic region	Year	Net or acoustic	Weight
N. capensis	Benguela Current	1982–1983	Net	DW
N. capensis	Benguela Current		Net	DW
N. simplex	Baja California; Mexico	1986–1993	Net	DW*
T. inermis	Barents Sea	1985–1989	Net	DW
T. inermis	Northeast Atlantic		Net	DW
T. inermis	Northwest Atlantic		Net	DW
T. inermis	Barents Sea		Net	
T. inermis	North Atlantic	1994	Net	
T. inermis larvae	Barents Sea		Net	
T. inermis larvae	North Atlantic		Net	
T. longicaudata	Barents Sea	Aug. 1985	Net	DW
T. longicaudata	North Atlantic	1994	Net	
T. longipes	Okhotsk Sea		Net	WW
T. macrura larvae	Antarctic, Indian Ocean	1985	Net	
T. raschii	Barents Sea	1985–1989	Net	DW
T. raschii	Northeast Atlantic		Net	DW
T. raschii	Northwest Atlantic		Net	DW
T. spinifera	British Columbia, Canada	1995–1997	Net	DW
T. spinifera	Baja California, Mexico	1993	Net	DW*
T. spinifera	British Columbia, Canada	1991–1997	Net	DW
T. spinifera	British Columbia, Canada	1991–1997	Net	WW
T. spinifera larvae	British Columbia, Canada	1995–1996	Net	DW
T. spinifera larvae	British Columbia, Canada	1991–1992	Net	WW

Note: DW, dry weight; WW, wet weight.
*Range of biomass values for day, night, and regional estimates.

FIBEX survey in 1980–1981 (Trathan and Everson 1994). Estimates of mean biomass per unit area (MBUA) based on FIBEX data range from 16 $g \cdot m^{-2}$ for the oceanic waters of the central Scotia Sea to almost 160 $g \cdot m^{-2}$ for the Bransfield Strait, which indicates distinct regional differences in krill biomass. These results have occasionally been interpreted to show that Antarctic krill biomass is much higher in shelf than in oceanic regions. However, Siegel et al. (1998*b*) pointed out that although in some years, this interpretation may be true, in other years, no significant difference in MBUA can be observed between shelf and oceanic waters. These authors found that significant differences occur in those years with above-average recruitment, when a strong juvenile year-class inhabits the shelf regions.

Results from Ukrainian Antarctic krill summer surveys (see Table 1) in the Prydz Bay region (Indian Ocean) indicate MBUA ranging from 17 to 187 $g \cdot m^{-2}$. East of this area (80–150°E), results from a single-season Australian survey indicate a krill MBUA of 5.54 $g \cdot m^{-2}$. Whether the difference in values between Prydz Bay and the eastern area indicates a consistent regional difference in krill density is uncertain, since data were collected in different years. However, the Australian survey data show distinct differences in average krill abundance between the eastern and western Indian Ocean sector of the Antarctic Ocean. These differences cannot be explained by a latitudinal abundance gradient. Historically, the entire sector has been viewed as relatively poor in krill (Marr 1962), but despite this, the area was successfully commercially fished by Japanese and Soviet Union fleets in the late 1970s and early 1980s (Pauly et al. 2000).

Estimates from Elephant Island and South Georgia show differences in variation of the same order of magnitude. Estimates range from 9 to 100 $g \cdot m^{-2}$ in the Elephant Island area and from 1.8 to 95 $g \cdot m^{-2}$ in the South Georgia area. Both these areas are the areas of main interest for continued commercial fishing.

From the Bellingshausen Sea, we have very little quantitative information on the krill stocks. In the summer of 1992–1993, Murray et al. (1995) estimated mean krill densities of 20 and 42 $g \cdot m^{-2}$ for two consecutive surveys. These are in the lower range of the values estimated during the FIBEX survey in 1980–1981 in the Atlantic sector and of the same order of magnitude as values found for open-ocean deep-water areas. Interestingly, much lower biomass has been observed in the Bellingshausen Sea than under the closed pack ice in the northern Weddell Sea. This latter area has generally not been believed to hold a high density of krill (Siegel and Harm 1996). However, it should be kept in mind that some of these data were collected over many years, while others represent single-season data. Thus, interannual differences can possibly camouflage between-region differences.

Other euphausiid species can attain average densities at least as high and even higher than *E. superba*, as shown by krill density estimates from net sampling surveys in Table 1. Species that occur in high densities (expressed as number of specimens per 1000 m^3) include *E. pacifica* in the Northeast

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Mean regional biomass or numerical density				
$g \cdot m^{-2}$	$g \cdot 1000\ m^{-3}$	$No. \cdot m^{-2}$	$No. \cdot 1000\ m^{-3}$	References
0.675–5.706	13–115		3 459 – 28 540	Barange and Stuart 1991
0.0004–0.072				Cornew et al. 1992
0.0007–0.116			406–9699	Gomez-Gutierrez and Robinson 1997
0.014–0.616	4–10	1.1–60.8	260–600	Dalpadado and Skjoldal 1991
	0.69–2.37		143–1093	Lindley 1980
	0.44–0.83		7–293	Lindley 1980
		115–207	250–600	Dalpadado and Skjoldal 1996
		1.2		Dalpadado et al. 1998
		520		Dalpadado and Skjoldal 1996
		13500		Dalpadado and Skjoldal 1996
0.019		1.7		Dalpadado and Skjoldal 1996
		10.0		Dalpadado et al. 1998
	82.8–214.8			Calculated from Gorbatenko 1996
			472	Hosie 1991
			<10	Dalpadado and Skjoldal 1991
	0.31–1.60		33–456	Lindley 1980
	0.61 –1.18		16–1183	Lindley 1980
0.148–0.394		20–35		Tanasichuk 1998*b*
0.000–0.171			16	Gomez-Gutierrez and Robinson 1997
0.326–1.185		34–145		Tanasichuk 1995, 1998*a*
2.639–13.985				Tanasichuk 1995, 1998*a*
0.083–0.607		450–7372		Tanasichuk 1995, 1998*a*
0.101–4.162				Tanasichuk 1995, 1998*a*

Pacific (>9000) and in the Northwest Pacific (>5000), *M. norvegica* in the North Atlantic (several hundreds), *Nyctiphanes australis* off Tasmania (>1000), *N. capensis* from the Benguela Current (>20 000), *N. simplex* off Baja California (>900), and *T. inermis* from the Barents Sea (>250) (Table 1).

Against these comparisons, it seems evident that the legendary large biomass of *E. superba* does not come from estimates of numerical or MBUA densities but from the huge area over which these densities occur and that finally result in such a high total population biomass. Since FIBEX, hardly any attempts have been undertaken to estimate the entire circum-Antarctic krill population size. The last biomass figure presented in the literature was about 400 Mt for the entire circum-Antarctic population of Antarctic krill size based on a review of earlier published estimates (Ross and Quetin 1988). Only recently, Nicol et al. (2000) used new information from mesoscale acoustic surveys around the Antarctic (taking into account the large geographical differences in krill density) to estimate the overall size of the circumpolar stock. Their estimates range from 60 to 155 Mt, which is substantially lower than the earlier estimates that did not take regional differences in krill density into account and were extrapolated from only the best-known areas, which seem to be those with the highest densities. The estimates given by Nicol et al. (2000) most likely also contain large uncertainties, since potential temporal, seasonal, as well as interannual differences in the biomass density estimates are not accounted for. However, the approach of Nicol et al. (2000) suggests that the size of the krill stock biomass is probably lower than previous optimistic views have indicated. An interpretation would be that the observed decline in the krill stock off the Antarctic Peninsula (see below) is indeed indicative of stocks in the entire Southern Ocean.

Seasonal variability in krill abundance

Basic to determinations of potential yield in a living resource is information on the seasonal and interannual distribution pattern of abundance and biomass. It is therefore important to note that the amplitude in krill biomass and abundance changes can be rather high. In *E. lucens* found in the Benguela Current, abundance may vary almost by a factor of 100 (Table 1). *Nyctiphanes australis* off eastern Tasmania also shows significant seasonal fluctuations and interannual variability, with a maximum biomass in autumn. In this species, the seasonal cycle is apparently driven by annually recurring summer intrusions of oligotrophic water from the subtropical East Australian and cooling and increase in production during autumn current (Blackburn 1980). Strong seasonal fluctuations in abundance and biomass have been reported for *E. pacifica* in Japanese inshore waters, which are seasonally affected by offshore waters. Numeric abundance of euphausiids peaks in March–April when larval density is high. Subsequently, abundance decreases due to high mortality of the early life history stages. During summer, currents transport warm (less productive) water from the south and presumably reduce abundance of cold-adapted *E. pacifica* in the region (Hirakawa et al. 1992). Despite the

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decrease in numerical abundance, biomass of the standing stock peaks in August–September due to growth during the summer season (Taki and Ogishima 1997).

The strong influence of seasonal currents is even more obvious around northeastern Japan. In February, *E. pacifica* biomass shows typical winter values (0.6 g·1000 m^{-3}). Two months later, in April, the cool Oyashio Current comes close to shore and krill biomass increases substantially (75–77 g·1000 m^{-3}) (Taki et al. 1996). In this case, the impact of younger stages produced by spawning in the spring can be neglected, since the increase in biomass is created by an increase in postlarval stages and primarily reflects advection of krill from more northerly waters. In years when a warm Kuroshio extension is pronounced, *E. pacifica* concentrations are found in waters deeper than 300 m whereas in normal years, the highest densities occur in shallow waters (Yamamura et al. 1998).

Substantial seasonal changes in *E. pacifica* biomass are also found in the Okhotsk Sea. In these waters, winter biomass exceeds the summer and autumn standing stock biomass by 4–55 times (Table 1). Drobysheva (1987, 1994) made similar observations for *Thysanoessa* species in subarctic regions of the Barents Sea. Fluctuations in *Thysanoessa longipes*, occurring in the same region as *E. pacifica*, were much lower between seasons (only by a factor of 2.5), with biomass peaking in summer. These latter results have the added value that they are based on net sampling at night and reduced net avoidance. Other species, such as winter-spawning *M. norvegica* in the western Mediterranean, also show abundance maxima during winter (Sardou et al. 1996). *Meganyctiphanes norvegica* as well as *T. inermis* off the Canadian east coast also show peak abundances in autumn–winter, but in this case, spawning takes place in spring.

Generally, it is assumed that the presence of winter maximum abundance reflects prespawning aggregations. This concept includes the idea that krill disperse during summer and adult mortality increases after spring spawning. Subsequently, growth and recruitment of juvenile krill increase over summer. However, the notion of high postspawning mortality and high growth rate is difficult to accept for euphausiids with a multiyear life cycle. It has to be checked carefully to what extent the seasonal fluctuation in abundance or standing stock biomass of a species is due to growth in weight, changes in natural mortality, or horizontal advection/migration. Vertical migration is believed to be governed by diurnal variations in light intensity, and in higher latitudes, this may tend to drive krill against the sea floor during summer, when the dark period is very short (Falk-Petersen and Hopkins 1981). Finally, sampling bias could also be caused by inadequate spatial coverage of the distribution range.

The complexity of seasonal variability in distribution and abundance is quite obvious for *E. superba*. In Antarctic krill, off the Antarctic Peninsula, the difference between the summer peak abundance and the winter minimum can be several orders of magnitude (Siegel 1988, 1989; Lascara et al. 1999). Figure 2 gives a conceptual view of the seasonal variation in *E. superba* off the Antarctic Peninsula developed by Siegel (1988).

Abundance of Antarctic krill is low in the region during winter, and the species' distribution is mainly confined to continental shelf waters west of the Antarctic Peninsula. In winter, the stock is composed of juveniles and immature as well as adult stages. From November onwards, both krill abundance and krill biomass increase rapidly and generally reach a maximum plateau at the end of December. The rapid increase in biomass cannot be attributed to growth alone, since numbers of krill in all size groups increase substantially during the same period. This phenomenon has been attributed to passive drift or advection into the area facilitated by the major oceanic circulation system. During the same period, krill distribution also expands beyond the continental slope into oceanic waters almost as far north as 59°S, although abundance north of 60°S is generally very low. Even when the stock has expanded the most, the distribution range does not reach the Polar Front.

During spring, a characteristic spatial separation develops, with juveniles inhabiting coastal waters, e.g., on the Antarctic Peninsula shelf, in Bransfield Strait, and in a narrow band extending across the northern shelves of the South Shetland Islands where a countercurrent flows from east to west in nearshore waters. These nearshore areas appear to serve as nursery grounds for the stock, while adult spawning stages primarily occur over the continental slope and in oceanic regions. The distribution area of medium-sized immature krill overlaps those areas occupied by the juvenile and adult portion, of the stock. Due to the larger size and higher swimming ability of the adult portion of the stock, it has been proposed that the establishment of an offshore spawning stock might be interpreted as an active offshore migration. This segregation of developmental stages can be seen as a habitat partitioning and allows the maintenance of high stock densities by minimizing intraspecific competition and parental cannibalism.

Normally, the peak in stock density and the wide distribution range persist until late February. In years of good juvenile recruitment, substantial differences in biomass have been observed. Ichii et al. (1998) reported 138 g·m^{-2} in inshore waters, while oceanic waters only held 8 g·m^{-2}. Spawning events may vary in length from 6 weeks to more than 3 months between years. The timing of the onset of spawning may also vary from December to February (Siegel and Loeb 1995; Spiridonov 1995).

From March onwards, krill abundance along the Antarctic Peninsula rapidly declines long before the advance of the winter pack-ice cover. Siegel (1988) related the decline in abundance to interrupted immigration rather than to postspawning mortality. The fact is that krill disappear from the oceanic region and the spatial succession of size and age groups ceases in autumn. Due to inshore/southward migration of adults, the oceanic regions eventually become abandoned by krill and both juvenile and postspawned adults are instead found together in shelf waters. Consequently, waters above the slope and in oceanic areas are left to the larval stages that are passively drifting under the influence of the West Wind Drift. This process can be seen as a second mechanism that partitions the habitat between developmental stages of *E. superba* during the seasonal cycle.

East of the Antarctic Peninsula – South Shetland Island region, segregated size groups of krill drift into the oceanic Scotia Sea, and the above-mentioned north–south succession of developmental stages and age groups seems to be maintained across the Scotia Sea (BIOMASS 1991). These ani-

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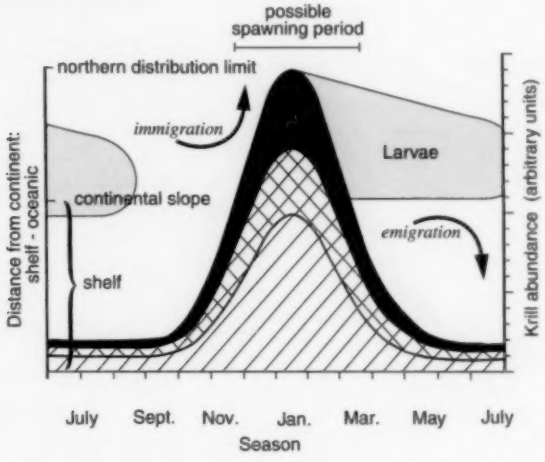
Fig. 2. Concept of the seasonal variation in *E. superba* distribution and abundance off the Antarctic Peninsula. Modified from Siegel et al. (1997).



mals are thought to belong to the Antarctic Peninsula stock and probably originate from the Bellingshausen Sea (Everson 1976; Siegel 1986, 1988). Krill in the upstream Bellingshausen Sea area show a similar pattern of geographically separated size and age groups (Siegel and Harm 1996).

This conceptual model of seasonal fluctuations in the *E. superba* stocks along the Antarctic Peninsula has been recently confirmed by seasonal investigations as a recurrent annual pattern for krill in the wider Antarctic Peninsula region (Lascara et al. 1999). The implications are clear; the ability to detect trends or quantify interannual and interregional differences in krill abundance and productivity depends on the appropriate comparisons. Time of data collection and the relative proportion of inner shelf, outer shelf, and slope within a survey region must be considered before comparisons with other measurements are made.

Interannual variability

From time series data, there is evidence that high interannual fluctuations in size of standing stocks of euphausiid populations are not the exception but seem to occur regularly around the world and in various species (e.g., Drobysheva 1994; Siegel et al. 1998*a*). These changes in abundance or biomass of krill stocks may be as high or higher than seasonal variations. For example, the stock of *E. pacifica* in the northeast Pacific exhibits a 5- to 10-fold change in biomass between years (Tanasichuk 1998*a*).

Nyctiphanes australis showed a 33-fold interannual change in numerical abundance and a 38-fold difference in biomass within a 3-year period (Blackburn 1980). It was suggested that this high interannual variability in stock size was generated by changes in the relative importance of the nutrient-poor and warm East Australian Current and a colder but nutrient-rich sub-Antarctic water mass separated by the Subtropical Convergence. Changes in the position and thus influence of the convergence have been associated with ENSO events (Young et al. 1993).

Another example concerns *M. norvegica* in the North Atlantic. This species is the most common euphausiid in Skagerrak and Kattegat. In Skagerrak, the abundance of *M. norvegica* varied as much as 5-fold during the period 1984–1992. In Kattegat, at the fringe of the distribution range of the species, variations were even higher (60-fold) (Ulmestrand and Hagström 1992).

Drobysheva (1987, 1994) reported that changes in density for the common Barents Sea species *T. inermis* amounted to 4–10 times the long-term average density. Implicitly, this means that the highest estimate was about 25 times higher than the lowest density value. This analysis was based on a unique long-term data set starting in the early 1950s that describes euphausiid distribution and abundance at high latitudes in the Barents Sea.

During a warm period between 1930 and 1950, *T. inermis* predominated among euphausiids in the Barents Sea. Concentrations were mainly found in the southern part and on the slopes of the banks. During the cold 1960s–1980s, *T. raschii* replaced *T. inermis* as the dominant component of the euphausiid concentrations. *Thysanoessa raschii*, however, was found more in the central to eastern coastal and northern slope areas. At the same time, the proportion of *M. norvegica* dropped from 17% of the total euphausiid stock to <1% (Drobysheva 1980).

Both Drobysheva (1994) and Dalpadado and Skjoldal (1996) argued that the fluctuations of the *T. inermis* stocks were controlled by predation, the reason being that stock size of *T. inermis* increased after the capelin stock dramatically declined during 1984–1987. During that period, the capelin stock was reduced from 5 to 0.1 Mt and the consumption of euphausiids was reduced from 29 to 7 Mt, thus leaving a high surplus of krill. In 1991, the krill stock briefly decreased after the recovery of the capelin stock (Drobysheva et al. 1992). However, a recurring low spawning stock of capelin from 1993 to 1997 may have changed the potential for krill recruitment and may provide a scenario for increases in krill stock again, as suggested by Saetre (1997). However, such an increase may be counteracted by a reduced inflow of Atlantic water and a increased transport of cold Arctic water with low-salinity conditions that have prevailed since the mid-1990s. Such conditions have been documented to have negative influences on the krill stock abundance in the Barents Sea (Drobysheva 1994). Since 1994, temperatures have been below average, ice conditions have been more severe, and, as a consequence, the wintering stock of euphausiids in the Barents Sea has dropped to half its biomass during recent years (Saetre 1997).

Some environmental conditions are strongly influencing the productivity of the water column and the species composition as well as the life history of krill populations. In some areas of the world, ocean upwelling conditions occur year after year as a regular seasonal event. In the longer term, these might be modified in their strength and duration by other events such as the ENSO effects and cause substantial interannual variations in krill stock size or composition.

In Californian waters, the biomass of *E. pacifica* and *N. simplex* can undergo 5- to 10-fold interannual changes (Brinton and Reid 1986). *Nyctiphanes simplex* has its centre of distribution further south and may account for 90% of the total abundance of euphausiids off Baja California (Gomez-Gutierrez et al. 1995). Even during weak ENSO events when the southerly influence is relatively strong, mean abundance

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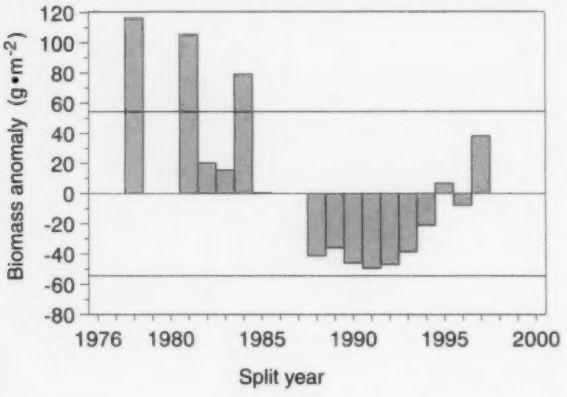
Fig. 3. Biomass anomalies for *E. superba* in the Antarctic Peninsula region. Bars indicate the upper and lower standard deviation of the mean. Split year 1990, for example, refers to the period from July 1989 to June 1990. Data source: Siegel et al. (1998*a*).



was five times higher than during non-ENSO years. Not only does the abundance of dominant species fluctuate during such events, but also, the entire euphausiid community structure changes to more subtropical/tropical components, replacing cold-adapted California Current species such as *E. pacifica* and *Thysanoessa gregaria* (Gomez-Gutierrez et al. 1995). During ENSO events (1957–1958, 1976–1978, 1981–1983, and 1986–1987), *E. pacifica* was never caught along the west coast of Baja California (Brinton and Reid 1986). Seasonal variation in the influence of different water masses and large-scale processes like ENSO events are responsible for a more vague and variable community structure and distribution pattern in these southern California to Baja California upwelling regions.

Thysanoessa spinifera is among the most common euphausiid species in the upwelling regions of the California Current. Off British Columbia, abundance of adult specimens declined continuously from 1992 to 1997. Larval abundance initially decreased but then increased from late 1995 to levels found earlier than 1992. High larval abundances were recorded despite low parental stock sizes in this region, indicating a lack of a clear-cut stock–recruitment relationship. Variability in adult stock size has been reported to vary by a factor of 7, while larval abundance varied by a factor of 16 between years (Tanasichuk 1998*a*). This author could not explain the stock decline by changes in growth, reproduction, or size composition; therefore, he argued that natural mortality increased due to higher consumption by Pacific hake. This predator prefers larger prey, and since adult *T. spinifera* is larger than *E. pacifica*, the effect of predation is greater on *T. spinifera*.

This partly explains why the adult stock of the sympatric species *E. pacifica* varies only by a factor of 2, while stocks of larvae vary by a factor of 6 over the same period. Fluctuations of *E. pacifica* were reported to be relatively small in the same region (Tanasichuk 1998*b*), despite that an El Niño event occurred during the investigated period. However, earlier investigations (Brinton and Reid 1986) have demonstrated that biomass of *E. pacifica* in Californian waters can vary by factors of between 5 and 10 between years.

Euphausia superba long-term variability

A time series of *E. superba* density estimates from net sampling surveys starting in the late 1970s indicates large interannual fluctuations in krill abundance in the Elephant Island – Antarctic Peninsula region (Fig. 3). Large krill catches were frequent during this early period but were only rarely seen during the 1985–1995 period (Siegel et al. 1997, 1998*a*). During the period 1990–1994, the krill stock showed low abundance levels. After a short recovery of the standing stock in the mid-1990s, abundance and biomass declined again. Thus, although estimates differ in absolute values due to methodological constraints, the biomass density variation pattern over the sampled period is similar regardless of whether data are based on acoustic or net sampling.

Ignoring extreme values from this time series, the *E. superba* stock in the area still fluctuates between years by a factor of about 21 times in biomass and 23 times in density. When yearly values of highest density or biomass are compared against the long-term average of the entire series, the variation is consistently less than three times the average (Table 2).

Although the above-described change in abundance and biomass was about one order of magnitude, Siegel et al. (1997) found it difficult to determine whether there is evidence for a persistent change in krill density since the early 1980s. An alternative could be that local krill abundance is subject to high degrees of variability. Regional abundance may vary to an extent and could persist for longer periods so that local fluctuations combine to produce a regional impression of a long-term decreasing trend.

Information from the mid-1990s clearly shows that the krill stock size briefly increased again towards formerly observed levels in 1996 and 1997 but dropped once more thereafter. This observation favours the explanation based on high interannual fluctuations in regional stock sizes and not the interpretation that assumes a persistent negative trend in krill density. The changes in abundance and biomass do not occur from one year to the next but seem to represent transient oscillations over a period of the order of at least 3–4 years. From Fig. 3, one could find indications of a cyclic event or a regime shift in the region, but these hypotheses certainly need more hard data before being generally accepted. The immediate reasons for the low stock size were seen in year-class recruitment variability, although low recruitment success had no significant influence on total stock density the following year (Siegel et al. 1998*a*). The reason for this is the multiyear class composition of the krill stock, which cushioned the krill stock against single-year poor recruitment (Siegel and Loeb 1995). However, in the case of succeeding poor years of krill recruitment, a response in stock size will become detectable over a period of subsequent years. Similarly, the stock seems to have the potential to recover within a period of 2–3 years with good recruitment.

Krill densities in areas both around South Georgia and around Elephant Island have been reported to fluctuate markedly between years. The changes in density occurred in the same direction at both sites (Brierley et al. 1999*b*). Unfortunately, annual acoustic estimates are only available from the period after 1990. The krill-rich period between the late 1970s and early 1980s was not routinely sampled by acoustics. However, even over this short period, results indicated a greater than 10-fold interannual variation in krill biomass off

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Table 2. *Euphausia superba* biomass index from acoustic and net sampling summer surveys in different areas of the Antarctic.

	Acoustic ($g \cdot m^{-2}$)			Net sampling, Elephant Island (Siegel et al. 1998*a*)	
Split year	Indian Ocean, Cooper Sea (Pakhomov 1995)	Elephant Island (Hewitt and Demer 1994; Brierley et al. 1999*b*)	South Georgia (Brierley et al. 1999*a*)	$g \cdot m^{-2}$	No.·1000 m^{-3}
1977	187.7				
1978	65.8			23.9	348.3
1979	60.7				
1980	20.5				
1981	20.0	68.5	59.7	31.2	161.4
1982	22.6		11.7	14.9	324.9
1983	21.3			14.0	276.7
1984	17.5	22.5		26.7	241.7
1985	41.1	8.4		11.0	85.9
1986	36.6		29.7		
1987	18.3	57.2			
1988	48.0	41.6		2.6	27.6
1989	92.0	82.4		3.7	79.8
1990	167.0	46.9	60.1	1.7	15.4
1991		23.8	6.4	1.0	6.5
1992		61.2	95.0	1.5	19.9
1993			65.8	3.2	29.2
1994		9.6	4.7	6.7	33.0
1995		27.8		12.2	73.3
1996		80.8	33.7	8.6	120.0
1997		100.5	39.9	17.1	212.5
1998		82.3	86.2	3.6	59.0
1999		23.7			

Note: Split year 1990, for example, refers to the period from July 1989 to June 1990.

South Georgia. It is worth noting that the values from 1994 off South Georgia are among the lowest reported acoustic estimates for *E. superba* and demonstrate a broad similarity with a variety of independent data sources like the concurrent poor krill abundance in the Peninsula area during the same year (Table 2) and the poor predator performance (breeding and survival success) during the same year around South Georgia (Brierley et al. 1997; Murphy et al. 1998). During the same year, a very low level of krill biomass was recorded for the South Orkney Islands (Brierley and Watkins 1996). Against this background and against the role that *E. superba* plays as the preferred prey for a number of predators, one may conclude that 1994 was a bad year for krill and krill-dependent species in the South Atlantic.

One may argue that these very low biomass values were caused by low recruitment in localized more or less self-maintaining stocks. Arguing against this interpretation is that *E. superba* has a long life span (>5 years) and the period over which the biomass variation occurred in this region was comparatively brief. Against this background, it does not seem reasonable to assume that the observed variations are produced by variations in recruitment in self-maintained stocks. If self-maintained stocks were present, one would expect the low biomass values to persist over several years. Instead, the magnitude and frequency of these variations indicate that changes in transport processes (advection/immigration) may be of great importance for the fluctuations in krill biomass observed in the South Georgia area and possibly other areas as well.

Fluctuations in year-class success in parts, or all, of the population across the Scotia Sea can generate large changes in the available biomass. The ocean transport pathways maintain the large-scale ecosystem structure by moving krill over large distances to areas where they are or are not available to predators depending on the predictability of this food resource. This large-scale physical system shows strong spatial and temporal coherence in the patterns of the interannual and subdecadal variability. The physical variability affects both the population dynamics of krill and the transport pathways, emphasizing that both the causes and the consequences of events at South Georgia are part of much larger-scale processes.

Conclusions

Three different categories of factors may control temporal and spatial changes in krill distribution and abundance: (*i*) physical factors, i.e., factors that govern the physical environment of krill such as temperature and circulation patterns either by creating boundaries for dispersion or by facilitating transport, (*ii*) population dynamics, e.g., breeding success, mortality, and recruitment of krill populations, and (*iii*) behaviour, i.e., horizontal or vertical migrations, which may create either increases or decreases in observed standing stock.

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Data on *E. superba* indicate that the populations have clear seasonal cycles in distribution and abundance (Siegel 1986, 1988; Lascara et al. 1999), which are probably influenced both by large-scale oceanographic parameters and by krill behaviour. Data from the FIBEX survey demonstrate regional differences (between shelf and oceanic regions as well as subareas of the Atlantic sector) in krill abundance as well as on a larger scale (between the Atlantic and Indian Ocean sector) during the same year and the same season (Trathan et al. 1992). The reasons behind these differences are still poorly understood but may involve both behaviour (horizontal and vertical migration) and physical factors (oceanic circulation generating drift and advection and eddies and meanders generating retention and concentration of krill). Finally, krill stocks display large interannual changes in abundance (Siegel et al. 1998*a*; Brierley et al. 1999*a*) due to variations in the success or failure of population processes such as breeding, recruitment, and mortality.

With regard to *E. superba*, the location of the Polar Front was thought to strongly influence meso- to large-scale abundance and distribution (Quetin et al. 1996). This may well be the case in the South Georgia region located close to the front. For other areas where krill occur well south of the Polar Front, however, this scenario seems less realistic. Recently, much larger-scale phenomena that may affect meso- to large-scale abundance of krill have become apparent. One such phenomenon is the variation in sea ice coverage caused by a circumpolar eastward procession of anomalies in winter sea ice extension with a periodicity of about 7–9 years moving around the Antarctic continent (Murphy et al. 1995; White and Petersen 1996). These cyclic events may, in the long term, be detectable in krill population processes. It might even be realistic to assume that strong amplitudes in these periodic changes could cause regime shifts and create instabilities in the krill populations.

Large-scale ENSO effects have been observed with a time lag of 50 months in the Atlantic sector of the Southern Ocean. These effects have been especially apparent in the straight outflow of the Drake Passage around South Georgia. The areas around South Orkney Islands and especially the Antarctic Peninsula show weaker signs of being affected by these "global ocean signals," possibly indicating that influences from other areas, like the Weddell Sea, may have local effects. Large-scale meteorological events also affect the location of pressure systems and consequently circulation patterns. For example, Naganobu et al. (1999) suggested that changes in the Drake Passage Oscillation index between the Antarctic Peninsula and South America influence sea ice formation, current velocities, and possibly krill advection.

Seasonal fluctuations in the magnitude observed for the long-lived *E. superba* in particular are unlikely to be explained by local or regional population processes such as mortality and recruitment. Instead, changes in such factors as advection (circulation patterns, currents, and fronts), extent of sea-ice cover, and behaviour (e.g., horizontal and vertical migration, swarming, and dispersion) are more likely to be responsible for changes in abundance and biomass in a given region over the course of the year. This may not necessarily mean that the area where any of these factors are operating is the same as the area in which the effect is observed. Instead, it seems more realistic to assume that mechanisms creating seasonal fluctuations in krill abundance, the proximate causes, are active, for example, in the upstream Bellingshausen Sea, while the effects are noticed downstream in the Antarctic Peninsula – Scotia Sea region. The combination of transport via advection and active horizontal migration has been shown to possibly govern changes in seasonal abundance levels as well as to affect the abruptness with which these changes may occur (Siegel 1988; Lascara et al. 1999).

Differences in estimates of stock biomass between areas within larger regions may also lead to misinterpretations because biomass may be redistributed by various processes within a region, i.e., it can be dangerous to assume that estimates of standing stock from individual areas are proportional to the regional standing stock. An illustrative example is provided by the occurrence of *E. superba* at the northernmost fringe of its distribution, around South Georgia. In some austral summers, low krill biomass in this area is just caused by southward displacement of water masses whereas in the central distribution range along the Antarctic Peninsula, biomass may be high and relatively stable. In other years, it might well be that low krill density around South Georgia reflects an overall low stock abundance. During such periods, the relative importance of shifts of water masses is diminished and interannual variability in biomass is probably governed by variations in population processes (reproduction, mortality, and recruitment). Thus, the system shows substantial similarities to the system described for *E. pacifica* off Japan were the standing stock varies due to the relative strength of the influence of the Oyashio and Kuroshio current systems.

Fluctuations in population parameters are often caused by food availability and quality. Changes in primary and secondary productivity create a potential for fluctuations in krill survival, probably causing reduced spawning success, increased larval mortality, and finally lower recruitment success. This results in instability in the krill population structure and affects variation in stock biomass. For long-lived species with one generation per year, this will lead to interannual changes in biomass, while seasonal fluctuations should be expected for short-lived species with several cohorts per year. Ultimately, changes in euphausiid productivity are caused by a combination of factors (climate effects, oceanography, food and prey availability, composition, competition, predation pressure, etc.). Different scenarios like changes in advection and productivity presumably go together like they do during strong El Niño events. Intrusion of warmer water masses into cooler regions replaces zooplankton communities, and at the same time, lower nutrients and primary productivity can cause substantial mortality in cold-water-adapted species, subsequently resulting in a declining stock size with a reduced distribution range.

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Understanding krill growth and aging: the contribution of experimental studies

Stephen Nicol

Abstract: Krill have been viewed as difficult animals to examine experimentally. Consequently, most information on growth and age of these pelagic crustaceans has come from demographic studies on preserved specimens. Only one species of krill, *Euphausia superba*, has been intensively studied in the laboratory, but the experimental findings on growth and age from these studies have fundamentally altered our perceptions of the population biology of this species. Most other species of krill remain in the preexperimental phase of understanding; thus, there remain considerable uncertainties regarding their growth and longevity. Unfortunately, these uncertainties are often ignored in ecological studies. In this paper, I have examined the role that experimental studies have played in increasing knowledge of the population biology of krill, particularly in the fields of growth and aging. I have indicated where discrepancies exist between field-based and experimental approaches and I outline some approaches for exploring these discrepancies and suggest some potentially fruitful areas for future research.

Résumé : Le krill est considéré comme un type d'animal difficile à examiner expérimentalement. En conséquence, la plupart de l'information sur l'âge et la croissance de ce crustacé pélagique provient d'études démographiques sur des spécimens conservés. Seule une espèce de krill, *Euphausia superba*, a été étudiée intensivement en laboratoire, mais les constats expérimentaux sur l'âge et la croissance fournis par ces études ont fondamentalement modifié notre perception de la biologie des populations de cette espèce. Pour la plupart des autres espèces de krill, les connaissances n'en sont qu'à la phase pré-expérimentale, et il reste donc des incertitudes considérables quant à leur croissance et leur longévité. Malheureusement, ces incertitudes sont souvent ignorées dans les études écologiques. J'examine ici le rôle qu'ont joué les études expérimentales dans l'accroissement des connaissances sur la biologie des populations de krill, particulièrement dans les domaines de la croissance et de l'âgeage. J'indique les points où existent des écarts entre les travaux de terrain et les méthodes expérimentales; je signale certaines approches visant à explorer ces écarts et je suggère des champs d'étude qui peuvent être fructueux pour des recherches futures.

[Traduit par la Rédaction]

Introduction

The significance of euphausiids (more commonly known as krill) in marine ecosystems has been recognized for centuries, particularly because of their obvious importance in the diet of baleen whales and many fish (Mauchline and Fisher 1969). Despite this recognized importance, until recently, few studies had examined the life history of any species of krill in detail. Even now, a review of the literature reveals that of the 85 species of krill, only 16 have been studied in the laboratory, and the overwhelming majority of studies reported have been of one species, Antarctic krill (*Euphausia superba*). Most studies of krill have concentrated on preserved samples from net sampling; the life history has been pieced together from measurements and observations of these preserved samples. Although early attempts had been made to keep krill in captivity (see Komaki 1966), it was not until the late 1950s that the first systematic experimental studies of live krill were reported. To this day, the majority of euphausiid species have not been studied alive, and experimental studies on growth rates have only been reported for 15 species.

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Although krill have been viewed by many marine biologists as merely plankton, many of the early records of their occurrence focussed on their behavior and on the features that make them truly nektonic rather than planktonic. Because many species of krill form surface swarms in the daytime, they can be observed in their natural habitat more readily than many pelagic organisms. This has led to many vivid descriptions of krill swarms and schools and to observations on behavior in the field that are rare in pelagic organisms prior to the advent of diving and the use of submersibles (Bigelow 1926; Hardy and Gunther 1935; Marr 1962). The descriptions of their complex behavior when in swarms have not generally been translated into interpretation of samples collected during net surveys or into the way in which such surveys are conducted. Marr (1962), during the "Discovery Investigations" into Antarctic krill, is one author who obviously had great difficulty in relating the results of his sampling program to what he knew of the behavior of krill from direct observation, and he devoted large tracts of his seminal report to this problem. Since then, the problems of relating the results of field-collected samples to observed behavior have been alluded to but have largely been sidestepped in practice (Nicol 1986; Watkins et al. 1990). Similarly, laboratory investigations into the biology of krill have produced results that often contradict or raise questions concerning the results of field sampling programs, yet the results from these two essential elements of biological investigation have not yet been integrated. Studies of growth and

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aging in krill are classic examples of where field and laboratory studies have taken divergent paths where the problems in each approach have been recognized but not reconciled. In this paper, I have outlined the contribution made by experimental studies to our overall understanding of growth and aging of krill. I have also highlighted what appear to be the areas of research where breakthroughs are necessary if we are to integrate the results of both field and laboratory studies to produce a better understanding of the biology of krill. Because the results of studies on the growth and aging of krill have been reviewed in depth recently (Siegel and Nicol 2000) I have focused on techniques and approaches used to study live krill rather than on the results of individual studies.

Background

Until the 1970s, krill of all studied species had been aged by measurements of length, and the population dynamics were described from these measurements. An upsurge in interest in krill biology in the late 1970s was largely associated with the SCAR/SCOR BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks) program, which aimed to improve the understanding of Antarctic krill because of the expanding fishery (El-Sayed 1994). Although the main aim of the BIOMASS program was to obtain an estimate of Antarctic krill biomass, perhaps the major legacy of this program will be its facilitation of a range of experimental studies that led to a questioning of many of the basic underlying concepts of the biology of Antarctic krill and, by extension, of that of all other euphausiid species (Nicol 1994). The full implications of this upheaval have yet to be fully appreciated.

Prior to the commencement of the BIOMASS program, several experimental studies of a variety of species of krill had been published. These early studies indicated the feasibility of studies on live krill and the utility of these studies to understanding their population dynamics (McWhinnie and Marciniak 1964; Lasker and Theilacker 1965; Gopalkrishnan 1973). Consequently, as BIOMASS gathered momentum, so did the study of live krill. Many advances in our understanding of the biology of Antarctic krill were a result of the establishment at about this time of onshore laboratories in which krill could be studied and of the use of shipboard laboratories to examine the physiology and behavior of living krill. Significantly, when the First International Symposium on Krill (which focused on Antarctic krill) was held in 1982 in the wake of the First International BIOMASS Experiment (FIBEX), six of the 23 papers published dealt with experimental studies or with studies on live krill (George 1984). As a measure of recent progress, 20 of the 77 presentations at the Second International Krill Symposium dealt with experimental studies or with studies on live krill.

Field measures of growth and age

Growth

The most frequently used method to estimate krill growth rates is by the analysis of sequential length–frequency plots from samples obtained throughout all or part of a seasonal cycle (e.g., Falk-Petersen 1985; Siegel 1987; Dalpadado and Skjoldal 1996). Such studies have most frequently used widely spaced sampling intervals; interpreting observed changes in size depends on the assumption that the same population is being repeatedly sampled. Only two studies have been reported that track changes in the mean length of identified krill populations over short periods of time. An aggregation of Antarctic krill that was followed, apparently migrating southwards for 12 days, exhibited a change in mean length corresponding to an average growth rate of 0.063 mm·day^{-1} (Kanda et al. 1982), a growth rate similar to that measured for this species in other studies (Nicol et al. 1992). In the other reported study, the modal length of a population of Antarctic krill sampled at South Georgia changed considerably over a 6-day period corresponding to a growth rate of 0.33 mm·day^{-1} (Clarke and Morris 1983). This estimated growth rate is far higher than others reported for this species.

In some species, the use of localized populations in fjords or embayments may ensure that a single population is sampled throughout a seasonal cycle (Astthorsson 1990); however, studies in these types of system have still had to imply immigration and emigration to explain the observed population trends (McClatchie et al. 1991).

Although most studies into the growth of krill have used sequential length–frequency analysis (Siegel and Nicol 2000), a number of different techniques have been used to separate size-classes from which the growth rates can be measured and ages can be estimated. These include the use of probability paper (Kulka and Corey 1978), Macdonald–Pitcher (or MIX) analysis (Pakhomov 1995), programs such as MULTIFAN and ELEFAN (McClatchie et al. 1991), and more recent models for estimating krill recruitment such as MLMIX (de la Mare 1994). Each of these approaches has its own proponents and produces slightly different results, but no attempt has yet been made to effect an intercomparison. Although the analysis of length–frequencies has become more sophisticated and robust recently, there are still enough uncertainties regarding the sampling problems and the relationships between the size of krill and their age (see section on age determination) that alternative approaches are still necessary to provide additional perspectives on growth rates (Ettershank 1984).

Sampling

Field-based methods for examining the biology of krill have generally used net-collected samples of krill from surveys that used a variety of designs ranging from single samples collected in a time series to large-scale surveys with many net tows conducted only once at each location. The population dynamics of krill are then determined based on morphometrics and classification of sex and maturity stages with the animals collected from these surveys.

There are a number of methodological problems with net-based surveys that have not yet been fully resolved (Miller and Hampton 1989). Some of these problems result from the use of the nets themselves (Omori and Hamner 1982). Nets are thought to be selective when dealing with euphausiids; fine-mesh nets may collect younger stages well, but the larger animals are thought to evade them (Wiebe et al. 1982), whereas large-mesh nets collect large krill but allow many of the smaller stages to escape (Brinton 1967). This

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problem increases with the size difference between the stages of krill and is probably at its worst for large species such as Antarctic krill. Net avoidance is thought to be partially visually stimulated, and attempts have been made to circumvent this problem by trawling at night (Everson and Bone 1986), by using darkened nets (Sameoto et al. 1993), and by avoiding the use of smaller nets. There is, however, no consensus on the degree to which nets are capable of collecting a representative sample of a population of krill. Unfortunately, there are no regularly used techniques that can provide samples of krill for analysis or laboratory study other than nets, so most surveys rely on their use for demographic studies.

There are also uncertainties regarding the degree to which net surveys provide a representative sample of the population. This is partially because krill are pelagic, often schooling organisms that can occur in patches in huge abundances (Miller and Hampton 1989). Some species of krill are known to segregate into aggregations of different size and maturity stages (Nicol 1984; Watkins 1986); thus, single point samples from an area may well not be characteristic of even the local population. High sampling density is the best guarantee that a synoptic picture of a krill population can be approached. However, ensuring that the same population is sampled over time is often more problematic. For many open-ocean or shelf species, there is no certainty that the same population is being sampled from one survey to the next.

In the Antarctic, the prevailing theory is that Antarctic krill are subject to flux, being moved quite rapidly from one area to another by large-scale ocean currents (Murphy et al. 1998). To assess changes in Antarctic krill populations, therefore, the assumption must be made that population processes inferred from small-scale surveys are affected by processes on a very much larger scale. However, neither this assumption nor the underlying flux hypothesis has yet been rigorously tested. Indeed, there is evidence for Antarctic krill of significant retention on the continental shelf (Ichii et al. 1998; Lascara et al. 1999) and of genetic subdivision of the population (Zane et al. 1998), which may indicate that the rate of exchange of individuals between populations may be slower than has been thought.

Although these assumptions have not been explicitly stated for other species of krill, interpretation of the results from most krill surveys seems to assume that the sampling regime is adequate (e.g., Boysen and Buchholz 1984; Tanasichuk 1998). A key area for making progress in understanding krill population dynamics will be the development of an understanding of the accuracy of the techniques that we use to sample krill populations. Further, because an understanding of how krill populations interact with the water masses that they inhabit underlies many of the other sampling problems, we will also have to understand this better. This may require a new generation of interdisciplinary investigations involving marine ecologists, coastal oceanographers, and modelers.

Experimental studies of growth and age

Experimental research into the biology of krill is a recent development. The first known results from experimental work on live Antarctic krill published were those of Fraser (1936), who observed spawning by captive animals onboard the RRS *Discovery II*. Mackintosh (1967), who reported some results on molting intervals of Antarctic krill kept at South Georgia, was the first to provide advice on how to keep this species alive for experimental purposes, and his experiments may actually have preceded those of Fraser (1936), since they were carried out some 37 years prior to publication!

The true dawn of experimental research on the biology of Antarctic krill occurred with the work of McWhinnie in the early 1960s, which began by reporting the first measurements of oxygen consumption by krill made onboard the RV *Eltanin* (McWhinnie and Marciniak 1964) and was followed by a series of experiments in the laboratories at Palmer Station on the Antarctic Peninsula that included observations on molting and growth, including shrinkage. About this time, results of experimental research into other species of krill were beginning to be published (Lasker and Theilacker 1965; Jerde and Lasker 1966; Paranjape 1967), but the field of experimental krill biology could be summarized in one short paper (Komaki 1966). The success of experimental studies on krill has depended on the ability to maintain them alive for appropriate periods in laboratories on land or on research vessels. The increasing sophistication of the laboratory facilities available on research vessels and onshore and the development of reliable methods for the transportation of live krill have been a major factor in our burgeoning knowledge of the biology of living krill (Ikeda et al. 1980).

Initial reports of studies on live krill emphasized the difficulties of keeping them alive in captivity (Baker 1963; Komaki 1966; Mackintosh 1967). Nonetheless, there have been successes with maintaining some species of krill through parts of their life cycle. Antarctic krill (Ikeda 1984; Ikeda and Thomas 1987*a*) and *Euphausia pacifica* (Ross 1981*a*, 1981*b*) have been reared from eggs to adults. *Euphausia crystallorophias* (Ikeda 1986), *Nematoscelis difficilis* (Gopalkrishnan 1973), *Nyctiphanes capensis* (Pillar 1985), and *Euphausia lucens* (Pillar 1984) have been reared through significant parts of their life cycles. However, the paucity of experimentally derived data for most species of krill has meant that estimates of growth rates, development rates, and longevity are still based on the analysis of preserved specimens.

Growth

Laboratory studies have a number of inherent problems that encourage caution when extrapolating their results to the wild population. Euphausiids are pelagic organisms, so their collection and confinement in an experimental apparatus imposes obvious stresses, and there are considerable difficulties involved in inducing natural behavior in the laboratory (Strand and Hamner 1990). Many species of krill, including all of those that have been experimentally studied, are aggregating or schooling organisms, and their experimental manipulation in isolation may inflict unrealistic conditions on them. Indeed, the whole field of krill behavior and how it affects experimental results is a field of study that has been largely untouched (Hamner and Hamner 2000). Despite these reservations, laboratory investigations allow detailed and controlled studies of variations in key processes such as growth and development that are not possible in the field

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(Ikeda 1985). One of the most important roles of experimental research is to examine the premises and findings of field-based studies so that their results can be interpreted in the light of the known capabilities of the animals.

Because of their small size, pelagic habit, high abundance, and frequent molting, krill are not amenable to mark–recapture studies, so field-based experiments on the growth and maturity of individuals have rarely been attempted. Successful intermediate-scale, or mesocosm, studies have only been reported twice (Price 1989; Pauly and Penrose 1998), although unsuccessful attempts have been made to utilize large-volume containers to examine the population dynamics of large groups of krill in the field (S. Nicol, unpublished data). Problems with working with very large containers include the ability to obtain enough animals to make the experiments worthwhile, maintaining realistic stocking densities, providing realistic amounts of food to encourage natural processes, and maintaining water quality. Consequently, experimental investigations on krill have been generally restricted to small-scale laboratory studies, and such studies into population parameters of krill have been confined to a small number of species.

The measured growth rates of krill, derived from a combination of field and laboratory studies, have been summarized recently (Siegel and Nicol 2000). An overwhelming number of experimental determinations of growth rates have been conducted on Antarctic krill. Most laboratory growth studies have relied on measurements of length taken from consecutively molted exoskeletons, which give a coarse-scale picture of growth over a whole molt cycle. These experimental studies have produced a wide range of measurements that have related growth rates to environmental factors such as food and temperature. They have also examined the factors that influence the main features of growth in krill, which include the intermolt period and the growth increment (Sameoto 1976; Ikeda and Thomas 1987*b*; Buchholz 1991). Temperature is a major factor influencing the rate of molting in all species of krill, and the intermolt period can vary considerably within a very narrow temperature range. For example, at 0°C, the intermolt period of Antarctic krill is of the order of 27 days (Nicol and Stolp 1991), but at 2°C, it can be as short as 17 days (Buchholz 1991). The intermolt period is also affected by the size of the animal. Small krill species generally molt more rapidly than larger ones, and smaller juvenile krill molt more rapidly than larger adults of the same species. This difference in molting rates between small and large krill may allow smaller animals to adjust their body size to local food availability on a short time scale. On longer time scales, the intermolt period of krill may change seasonally, increasing in winter and shortening in summer. Seasonal variation in molting rates has only been demonstrated for Antarctic krill (Thomas and Ikeda 1987), but this is probably only because other species have rarely been maintained for a full year. The endogenous and exogenous factors that control growth in any species of krill have received only cursory attention, and this is an area that will require future research if we are to make progress in understanding krill life histories.

Longevity

Because there are so few studies that have either reared krill from eggs or have maintained them alive in captivity for extended periods, there are only laboratory data on longevity available for Antarctic krill (Ikeda and Thomas 1987*a*). These experiments indicated that krill could survive in captivity for many years, and based on experimental observations, Ikeda (1985) proposed a maximum life span for this species of around 11 years. This projection was considerably greater than the generally accepted 2- to 3-year life span of krill from field-derived samples (Mackintosh 1972), and again the discrepancy between the laboratory and field data remains to be resolved. There is now, however, a general acceptance that Antarctic krill do live longer than the 2–3 years initially suggested (Siegel 1987), but how many substantial year-classes exist in the population at any one time is still a matter for clarification. Although the key question is not "how long krill can live?" but "how long does an average krill live?," experimental studies have indicated that the range of possibilities is wider than was previously thought. These findings also stimulated a number of studies into other methods for aging krill to determine whether there were additional age-classes in the population that were being missed by conventional length–frequency techniques.

For a commercially harvested species such as Antarctic krill, knowledge of the age structure and life span is critical for the development of management approaches. In light of the radical reevaluation of the biology of Antarctic krill that occurred following the results of laboratory studies into its longevity, age, and growth, it is therefore surprising that similar studies have not been conducted on other key krill species, particularly those that are also commercially harvested or have commercial potential such as *E. pacifica* and *Meganyctiphanes norvegica* (Nicol and Endo 1999).

Instantaneous growth rate: linking field and laboratory studies

A methodology for the measurement of instantaneous growth rates (IGR), the measured growth rate of live, freshly collected krill, was outlined by (Quetin and Ross 1991), and their results demonstrated both growth and shrinkage in individual Antarctic krill (Ross et al. 2000). This technique was modified (Nicol et al. 1992) to examine the effects of capture on the measurements of growth rate and subsequently to increase the sample size (Nicol et al. 2000). This technique is beginning to provide data on the growth rate of a wide range of sizes of Antarctic krill that can be related to environmental conditions and to the observed changes in the size of the whole population (Nicol et al. 2000; Ross et al. 2000).

The IGR technique relies on collecting live krill in good condition. Onboard, the krill are kept in individual containers and are checked regularly for molts during the 4 or 5 days following capture. During this period, the growth rate of krill appears to be stable and unchanged by maintenance conditions and is likely to reflect the natural growth rate; after 5 days, the growth rate starts to decline and begins to reflect the effect of confinement in the laboratory (Nicol et al. 1992). The growth rate is estimated from the difference in length of the uropods (or telson) on the molts and the whole postmolt krill. Since Antarctic krill molt every 20–30 days at 0°C (Buchholz 1991), only one in 20 to one in 30 krill will molt on any given day of the experiment, assuming that molting is random. This methodology therefore requires

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large numbers of animals of which only a small fraction will be used for actual estimates of growth rates. The key to obtaining greater numbers of growth rate measurements is to increase the number of krill that can be maintained individually at one time (Nicol et al. 2000). Using small (250 mL) perforated jars to hold individual krill in a large (1000 L) flow-through tank permits a sample size of over 1000 krill per experiment, a much larger sample size than has been the case in earlier studies.

The IGR technique has shown positive growth of adult Antarctic krill during the late summer and autumn, with increases in body length at molting of between 1.75 and 4.4% (Quetin and Ross 1991) and, in winter, shrinkage of between –0.16 and –2.03% of body length per molt. These growth and shrinkage rates are similar to those exhibited by krill in the laboratory (Ikeda and Dixon 1982; Ikeda and Thomas 1987*a*).

The IGR technique offers a method to estimate growth rates that can be compared with simultaneous length–frequency analyses from the same populations. This should allow some of the conflicting results on krill growth that have emerged from field and laboratory studies to be resolved. The technique is also being used to compare krill growth rates with environmental conditions, and such a study has recently produced a functional response curve relating krill growth rates to ambient food conditions (Ross et al. 2000). Although the IGR technique has been developed for Antarctic krill, it should be applicable to other species that are robust enough to withstand capture and experimental confinement. IGR experiments with both *E. crystallorophias* and *Thysanoessa macrura* have now been successful (S. Nicol, unpublished data), so it seems likely that this technique may be applicable to a range of krill species. For smaller temperate or tropical species, the more rapid molting rates may actually enhance the sensitivity of this technique by providing far greater sample sizes.

The problem of shrinkage

A major rethinking of the life history of Antarctic krill was initiated when it was demonstrated that krill could survive long periods of starvation (211 days) through utilization of body reserves and shrinkage (Ikeda and Dixon 1982). This experimental finding, which demonstrated that krill can shrink through molting if starved, raised suggestions that length-based aging methods might be subject to considerable error. All animals lose weight when starved. However, Antarctic krill were shown to reduce their size, in terms of the usual measures of length, in suboptimal food conditions through molting. Not only did krill molt to a smaller size, but they could also lose their secondary sexual characteristics over time (Thomas and Ikeda 1987). This finding introduced further uncertainties into the use of measures of length, combined with an assessment of sexual maturity, as definitive indicators of age. These results precipitated a debate on aging and mortality of krill that is yet to be resolved (Nicol 1994).

Further results of experimental studies on Antarctic krill showed evidence of shrinkage by populations of Antarctic krill in the laboratory (Nicol et al. 1991) as well as by individuals. Groups of krill with polymodal size distributions tended to contract to a unimodal size distribution at the lower end of the original size range when kept in aquaria under low food conditions (Nicol et al. 1991; Sun 1997). This alteration of the shape of the size spectrum may come about through the differing food requirements of the smaller and larger animals at low food concentrations: small krill receive a maintenance ration but the larger ones do not and hence shrink. This differential effect is most likely to cause difficulties in length–frequency analyses if it occurs under natural conditions.

Long-term food deprivation results in a relatively constant average shrinkage rate of 0.033 mm·day^{-1} (about –3.3% per molt cycle) in juvenile Antarctic krill (Ikeda et al. 1985). This figure is similar to the maximum rate of shrinkage demonstrated by Antarctic krill in IGR experiments that have been allowed to proceed beyond 5 days (Nicol et al. 1992). Thus, krill can apparently achieve their maximal shrinkage rate under food limitation within a matter of days and can maintain this shrinkage rate over very long periods (Ikeda and Dixon 1982). Somewhat surprisingly, populations of juvenile Antarctic krill in high summer, with IGRs at capture as high as 9% of their body length per molt, can commence shrinking after a period as short as 10 days (Nicol et al. 1992). Shrinkage is thus not merely a drastic response to long-term food deprivation in winter but can occur as a flexible response to a reduction in food supply at any time.

Although the issue of shrinkage has been discussed primarily with regard to Antarctic krill, the questions raised through these experimental studies are equally applicable to other species. There is experimental evidence that all species of krill so far examined can shrink in the laboratory (*E. pacifica* (Lasker 1966), Antarctic krill (Ikeda and Dixon 1982), *M. norvegica* (Buchholz 1985), *Thysanoessa inermis* (Dalpadado and Ikeda 1989), and *Nyctiphanes australis* (Hosie and Ritz 1989)). Additionally, many studies using length–frequency analysis have also shown evidence of a reduction in mean size over winter (Hollingshead and Corey 1974; McClatchie et al. 1991; Dalpadado and Skjoldal 1996). Studies on *E. pacifica* have also indicated that shrinkage can occur at any time of the year in response to short-term food shortages and may indeed be an energetic response to fluctuating food supplies (Marinovic and Mangel 1999). The ability of small, rapidly molting species to adjust their body size, and hence their energetic requirements, to ambient food supplies suggests that shrinkage is not merely an extreme response to a highly seasonal environment. The cautions expressed over the use of length–frequency analysis as the sole aging technique for Antarctic krill are thus relevant to other species and should stimulate further research into the relationships between size and age.

In most pelagic ecosystems, winter is the period when food is most likely to be limiting, and hence, this is the period when overall shrinkage of krill populations would be likely to occur. Antarctic krill captured under winter sea ice showed a decrease in mean size and a restriction in the size ranges of krill present (Kawaguchi et al. 1986). Kawaguchi et al. (1986) also found little evidence of feeding in the water column, low chlorophyll *a* concentrations throughout the winter, and oxygen consumption figures that corresponded to those of starving, shrinking krill (Ikeda and Dixon 1982). Antarctic krill in Admiralty Bay (Antarctic Peninsula re-

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gion) may show winter shrinkage (Ettershank 1983), but this change has also been attributed to water movements into and out of the bay, bringing krill of different origin and life history into the bay, and to differential size-related mortality (McClatchie et al. 1991). Individual Antarctic krill have been observed shrinking during winter using the IGR technique (Quetin and Ross 1991), although it is not certain whether shrinkage is a widespread or common enough phenomenon to significantly affect the mean size of the population. The major questions are how frequently (if ever) krill encounter food shortage sufficient to engender shrinkage and do they do so for sufficient periods to affect the size structure of the population. Only in situ studies in winter and spring will be able to answer these questions.

Krill are obviously capable of shrinkage, but when and where this occurs is a matter for further research. How such shrinkage affects the analysis of population dynamics of krill depends on whether the shrinkage occurs in a systematic fashion, preserving the year-classes, or whether it tends to merge year-classes. In analyses of krill populations, it should be recognized that they are capable of shrinking and that this should be taken into account as a potential source of uncertainty in life history models.

Alternative methods for measuring age and longevity

The search for alternative methods for estimating krill age and longevity arose from two findings from research into Antarctic krill. Firstly, laboratory studies showed that Antarctic krill could shrink in length and regress in maturity, both when starved (Ikeda and Dixon 1982) and during winter (McWhinnie et al. 1979), and that individual krill could live for many years going through cycles of growth and shrinkage (Ikeda and Thomas 1987*a*). Secondly, examination of the population size structure of Antarctic krill from net samples often revealed anomalies. Two length-classes were present, but the larger size-class was frequently far more abundant than the smaller size-class (Ettershank 1984), which suggested that the larger size-class actually represented several different age-classes that could not be separated by simple measures of length alone. Although shrinkage and anomalous size–frequency histograms have been observed in other species of krill, there has not been a concerted effort expended to develop alternative methods for species other than Antarctic krill. This emphasis on understanding the age structure of the Antarctic krill population resulted primarily from the need for accurate age-related information for the management of the Antarctic krill fishery (Nicol and Endo 1999).

A variety of aging techniques have been developed specifically for Antarctic krill or have been modified from those developed for other species. All of these approaches have had to surmount the problem that krill molt extremely rapidly (anywhere from every 4 to every 40 days) and continue to do so throughout their life cycles. At ecdysis, most of the animal's hard parts are shed, and it is in these hard parts that records of age are frequently laid down in other species. Consequently, effort has been put into developing chemical measures of age or into detecting more subtle morphological changes that occur with age but that are not reversible when general body shrinkage occurs. Considerable effort has also been put into refining the techniques for distinguishing peaks in length–frequency histograms so that better length, and hence presumably age, discrimination can be achieved.

Age pigments

The prospect of Antarctic krill shrinking during winter prompted investigations into the use of fluorescent age pigment accumulation as an indicator of age (Ettershank 1983). Fluorescent age pigments, including lipofuscins, are substances that accumulate with time in the cells of all organisms so far examined (Hammer and Braum 1988). They are thought to be the products of cellular lipid peroxidation processes, accumulating at a rate dependent on the metabolic rate of the animals. They emit light at 420–470 nm when excited by wavelengths of 340–370 nm. Initial studies indicated that fluorescent age pigments held promise as an indicator of age (Ettershank 1983). Laboratory studies with Antarctic krill indicated that some soluble fluorescent age pigments accumulated with age in a population that shrank significantly in length over a period of a year in captivity (Nicol et al. 1991). There are, however, a number of demonstrated methodological problems that have raised doubts about the utility of using soluble age pigments as an indicator of age. The use of chloroform–methanol extraction for the quantification of liposfucin (or fluorescent age pigments) has been shown to be problematic because of formaldehyde-induced enhancement of fluorescence (Nicol 1987), interference products as a result of sample processing and extraction, temperature effects on the resultant fluorescence (Hill and Wommersley 1994), loss of soluble age pigments at molting (Hirche and Anger 1987), a poor relationship with morphological lipofuscin, and the uncertain chemical nature of the pigments involved (Sheehy 1996). Age pigments also accumulate with metabolic time rather than chronologically, so environmental effects on metabolism can have a marked effect on the rate of pigment accumulation (Wahle et al. 1996).

Studies on captive populations of species of crustaceans other than krill have shown significant accumulation of age pigments when examined using image analysis and fluorescence microscopy (Sheehy et al. 1994; O'Donovan and Tully 1996; Wahle et al. 1996) or confocal microscopy (Belchier et al. 1994), and these techniques might prove more reliable than the solvent extraction method if applied to krill. Future attempts to use age pigments will require experimental manipulations to determine the possible effects of exogenous and endogenous factors on the rate of pigment accumulation. Further chemical identification of the exact molecules responsible for the age-related fluorescence may lead to more efficient and precise techniques for aging using age pigments. However, it seems unlikely that the rather time-consuming methodologies for quantifying levels of fluorescent age pigments will supplant more convenient and simpler morphometric measures. Their main use may lie in their ability to ground truth morphometric measures.

Multiple morphometrics

Studies on Antarctic krill and *T. macrura* have attempted to use multiple morphometrics to obtain more information on krill population age structure than can be obtained by conventional length–frequency analysis (Ettershank 1984;

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Farber-Lorda 1994). Although these approaches have yielded some preliminary results in separating groups of adults of both sexes, they have not been developed much further. The advent of image analysis may make such techniques more appealing in the future.

Eyeball size

A novel approach to aging in Antarctic krill has involved utilizing some measure of the size of the eyeball relative to body size (Sun and Wang 1995, 1996; Sun et al. 1995). The premise of this approach is that the compound eye is a complex structure and would be conserved if the animal is shrinking. Consequently, the eye of an adult krill that had shrunk would be relatively larger compared with the eye of a juvenile of the same size that had being growing. The initial results of this approach showed that laboratory-shrunk Antarctic krill had relatively larger eyes (from crystalline cone counts) than would be predicted from their overall body length. Further, the number of crystalline cones in the eyes of krill caught in November (following the most likely period of food scarcity and hence the greatest likelihood of shrinkage) was higher than might be predicted for their size, and the ratio of the crystalline cone count to body length resembled that of shrunken laboratory krill (Sun et al. 1995). Subsequently, measurement of the eyeball diameter has been shown to be a good (and less tedious) substitute for crystalline cone counts, and eyeball diameter appears to remain constant when krill shrink in the laboratory (Sun and Wang 1996; Sun 1997). The critical test of this technique is to determine whether the eye of a krill that has been shrinking begins to grow again once the krill begins to increase in size or whether the krill has to reach its former preshrinkage size before the eye begins to grow in size again. If the former happens, then frequency histograms of eyeball diameter should be able to reveal age-classes. If, on the other hand, the latter case holds true, then the usefulness of this technique may be restricted to distinguishing between a real juvenile and a shrunken adult of the same size. Although this technique has shown promise, there are no recent reports of attempts to apply it to field samples from other areas. One important practical outcome of this method is that it appears possible to use the crystalline cone number or eyeball diameter to distinguish older krill from new recruits because it can discriminate between small krill that have not shrunk and krill that are small as the result of body shrinkage. This is sufficient information to estimate the key parameters of recruitment and mortality (de la Mare 1994) for the model used by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) to manage the Antarctic krill fishery.

The way forward: integrating field and laboratory studies and the use of models

Studies into the growth and age of krill of all species have taken two separate paths: experimental and field based. Very often, the significant results of the two approaches have not been adequately integrated. Results are dismissed merely as "laboratory artifacts," "experimental manipulations," or "sampling bias." There is sufficient evidence available now to unequivocally assert that there are problems involved with the study of growth and age of krill that cannot be addressed by the currently used techniques and certainly cannot be addressed by either field studies or experimental studies in isolation.

Experimental and field studies of growth in krill will have to be compared. This could be achieved by repeatedly sampling a known population over a restricted time period (about 1 month) while at the same time conducting growth experiments such as IGR measurements. Such an approach would either begin to give us confidence that our approaches are achieving the same aim or point out further anomalies that would have to be addressed.

To compare growth rate measurements, however, some standardization of measurement will be necessary. In a recent review of krill population dynamics (Siegel and Nicol 2000), no fewer than eight different units of growth were used (milligrams wet weight per day, percent wet weight per day, milligrams dry weight per day, milligrams carbon per day, percent dry weight per day, millimetres total length per day, millimetres per moult, percent size change at molt), and many of these further depend on relationships between the measured parameters (such as dry weight) and other frequently used measures (such as total length). These morphometric relationships have been shown to be far from simple in themselves (Morris et al. 1988). Additionally, because of the known environmental and ontogenetic effects on growth, it is difficult to compare one measure with another even when the same technique is used. Perhaps the various measurements could be compared for a "model krill" species, for which a growth model can be constructed, to provide the basis for understanding the critical aspects of growth in all species of krill.

There have been few attempts to model krill growth or life history (Astheimer et al. 1985; Rosenberg et al. 1986; Rumsey and Franks 1999), and there is the need for the development of growth models that incorporate some of the features known about krill from experimental studies. Specifically, there are currently no lifetime growth models for krill that incorporate what we know of changes in growth rates with age, coupled with seasonal effects on the physiology of molting and on the food supply.

Intercomparisons between the various statistical routines used to separate age-classes, using both real and model data, would assist in standardizing an approach to the understanding of the population dynamics of krill from field samples. Using experimental data to parameterize these techniques, as has been done for Antarctic krill, would also lead to a better understanding of the life history of some of the less well-studied species.

A source of useful data, particularly on growth, for the future may be the fisheries for krill. There has been a recent tendency to obtain more information from commercial catches (Kawaguchi et al. 1997), but there is scope for an expansion of this role. Krill trawlers in the Antarctic often remain with a single swarm for days or weeks, repeatedly fishing it. There has only been one published account of growth estimated from these operations (Kanda et al. 1982). Because the Antarctic krill fishery operates year-round (Nicol and Endo 1999), there is the opportunity for the collection of growth rates for seasons other than summer.

Perhaps the assumption that has most impeded progress in

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understanding krill biology is that that views krill as "merely plankton." Unfortunately, the term "micronekton" is cumbersome, but until krill are recognized as being a class of organisms fundamentally different from the "small drifting animals" of plankton, we will continue to misunderstand their biology. This persistent misclassification has allowed the continuation of inappropriate sampling strategies, the application of unrealistic experimental regimes, and the comparison of krill with "other zooplankton" such as copepods. Krill are not entirely unique and they have far more in common with organisms such as pelagic decapods or mysids than they do with truly planktonic copepods.

Krill have often been viewed in isolation from other truly analogous crustaceans, yet there are valuable sources of information on crustacean life history and physiology that have been gathered from crustacean species that have a history of experimental research or that are of more direct economic use. In particular, there have been great advances in understanding the growth of penaeid prawns since they became heavily utilized in aquaculture, and information on these not dissimilar organisms may be of use in understanding the outstanding problems in krill biology.

Perhaps the emphasis on Antarctic krill has perpetuated problems in krill biology. For too long, we have been able to use the premise that we are dealing with a unique species that experiences singular environmental challenges so that we can study it in isolation from other species. Few studies on Antarctic krill ever reference other species of krill, let alone other crustacean species. Many of the existing problems may be tackled by assuming that all species of krill are very similar and that the processes of growth, aging, and development are very similar among species. This approach could allow the selection of some model populations, possibly within quasi-enclosed water bodies, for concerted study to test various hypotheses, and the results of these studies could be then applied to other species to test the validity the initial assumptions.

Conclusion

Although the importance of krill in the marine economy has been recognized for centuries, it is only in very recent times that we have been able to gain some appreciation of how individual krill and whole populations maintain themselves in their environment. Experimental studies have been critical in developing this awareness, and a deeper understanding of the ecology of these abundant and important crustaceans will only come from further experimental investigations coupled with systematic observations of living krill and advanced and informed sampling strategies. Perhaps an increased focus on the harvesting of krill in polar and temperate waters will give rise to a new upsurge in interest in these enigmatic crustaceans.

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Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill

Stig Falk-Petersen, Wilhelm Hagen, Gerhard Kattner, Andrew Clarke, and John Sargent

Abstract: Environmental seasonality is a critical factor in structuring polar marine ecosystems. The extensive data now available on the lipids of Arctic and Antarctic euphausiids show that all species are characterised by a seasonally high lipid content, and neutral lipids, whether wax esters or triacylglycerols, are primarily accumulated for reproduction. The Arctic *Thysanoessa inermis* and the Antarctic *Euphausia crystallorophias* contain high levels of wax esters and higher concentrations of 18:4(n–3) and 20:5(n–3) and a lower ratio of 18:1(n–9)/(n–7) fatty acids in their neutral lipids than the Arctic *Thysanoessa raschii* and the Antarctic *Thysanoessa macrura* and *Euphausia superba*. Large amounts of phytol in the lipids of *T. raschii* and *E. crystallorophias* during winter suggest the ingestion of decaying algae originating in sedimenting material or in sea ice. *Thysanoessa raschii*, *T. macrura*, and *E. superba* have a high ratio of 18:1(n–9)/(n–7) fatty acids, indicating animal carnivory. We conclude that *T. inermis* and *E. crystallorophias* are true high polar herbivores, while *T. raschii*, *T. macrura*, and *E. superba* are omnivores with a more boreal distribution. The Arctic species *Thysanoessa longicaudata* and *Meganyctiphanes norvegica* are carnivores feeding on *Calanus*, as indicated by high amounts of 20:1(n–9) and 22:1(n–11) fatty acids.

Résumé : Les cycles saisonniers de l'environnement jouent un rôle critique dans la structuration des écosystèmes marins polaires. La masse de données recueillies sur les lipides des euphausiacés de l'Arctique et de l'Antarctique montre que toutes les espèces se caractérisent par une forte teneur saisonnière en lipides, et que les lipides neutres, qu'il s'agisse d'esters cireux ou de triacylglycérols, sont accumulés principalement en vue de la reproduction. L'espèce arctique *Thysanoessa inermis* et l'espèce antarctique *Euphausia crystallorophias* présentent de fortes teneurs en esters cireux, et de plus fortes concentrations de 18:4(n–3) et de 20:5(n–3) mais un plus faible rapport des acides gras 18:1(n–9)/(n–7) dans leurs lipides neutres que l'espèce arctique *T. raschii* et les espèces antarctiques *T. macrura* et *E. superba*. La présence en hiver de grandes quantités de phytol dans les lipides de *T. raschii* et de *E. crystallorophias* pointe vers l'ingestion d'algues en décomposition provenant de matières qui sédimentent ou de la glace de mer. *T. raschii*, *T. macrura* et *E. superba* présentent un rapport élevé de 18:1(n–9)/(n–7) , ce qui indique une alimentation carnivore. Nous concluons que *T. inermis* et *E. crystallorophias* sont de vrais herbivores des hautes latitudes polaires, tandis que *T. raschii*, *T. macrura* et *E. superba* sont des carnivores à distribution boréale plus large. Les espèces arctiques *Thysanoessa longicaudata* et *Meganyctiphanes norvegica* sont des carnivores qui se nourrissent de *Calanus*, comme l'indiquent leurs fortes teneurs en acides gras 20:1(n–9) et 22:1(n–11).

[Traduit par la Rédaction]

Introduction

Pelagic algae and animals in polar seas are subjected to marked climatic changes over a wide range of time scales with fundamental implications for biodiversity and bioproduction. Polar systems are characterised by pronounced seasonal oscillations in incident solar radiation with the light climate changing dramatically during the year from a period of entire darkness lasting approximately 4.5 month at 80°N to a period of summer midnight sun. The ice regime also changes considerably on hourly, daily, monthly, yearly, and decadal scales (Murphy et al. 1995; Vinje 1999), strongly influencing the light available for primary production between seasons and years (Falk-Petersen et al. 2000). For example, the Barents Sea and parts of the Norwegian Sea were totally ice covered in the spring of 1966, whereas in 1995, most of these areas were ice free (Vinje 1999). Consequently, pelagic animals in high-latitude seas with marked variations in ice cover are exposed to a highly variable food supply, not only between seasons (Lee and Hirota 1973; Falk-Petersen et al. 1990) but also over periods of years to decades. Polar pelagic ecosystems are markedly unstable (Sakshaug 1997), and krill, being one of the major components of such systems, must therefore be adapted to an environment changing on different time scales.

Despite the fluctuating environment, marginal ice zones

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Fig. 1. Lipid dynamics (total lipid) of *T. inermis*, *T. raschii*, and *M. norvegica* in relation to season, reproduction, and the spring phytoplankton bloom. After Falk-Petersen (1981, 1988).

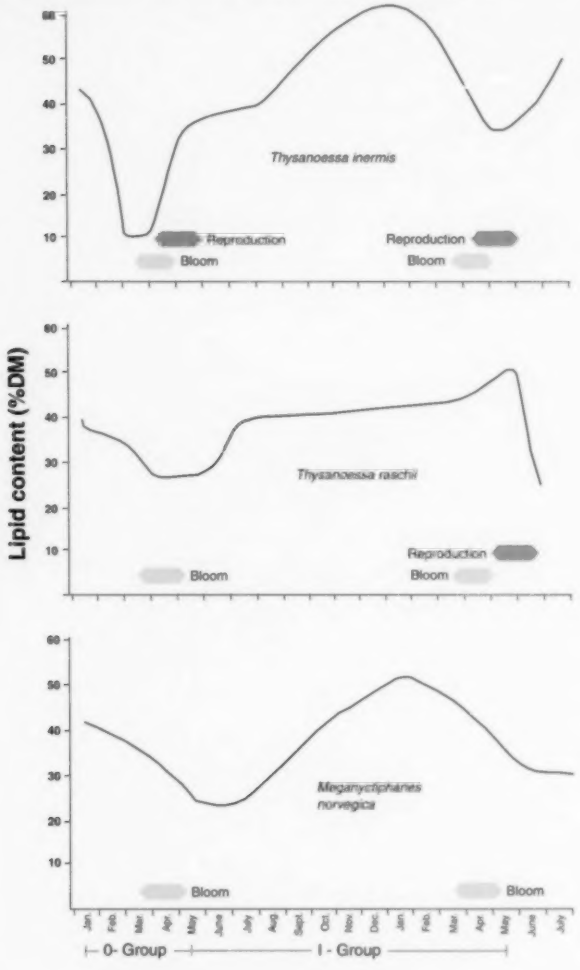
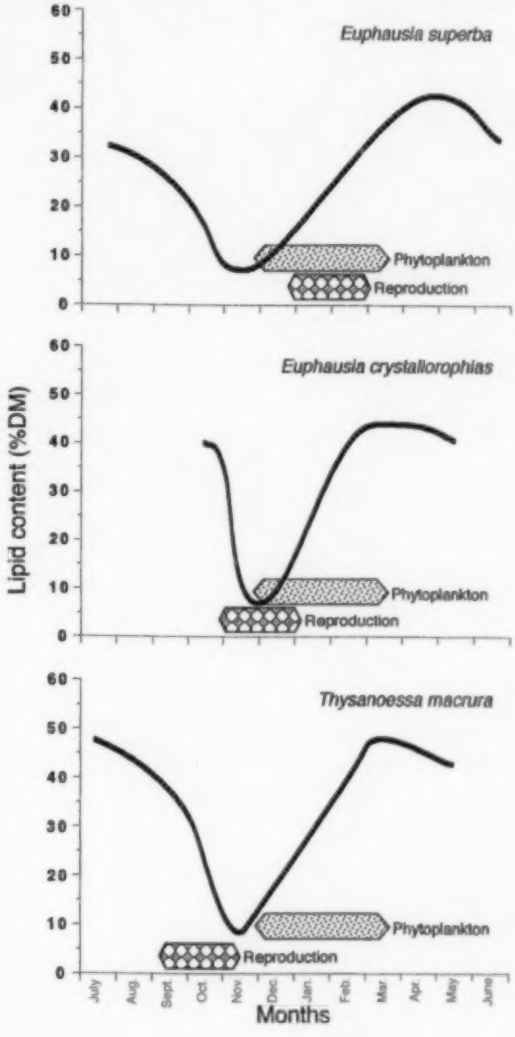


Fig. 2. Lipid dynamics (total lipid) of adult *E. superba*, *E. crystallorophias*, and *T. macrura* in relation to season, reproduction, and primary production. After Hagen et al. (1996), Kattner and Hagen (1998), and Hagen and Kattner (1998).



are often among the most productive seas of the Northern and Southern hemispheres with short, intense periods of primary production. Pelagic marine animals exposed to such marked variation in available food have generally adapted by storing large amounts of lipids as energy reserves. The level of lipid increases from 10–20% of the dry mass commonly found in phytoplankton to more than 50% in herbivorous zooplankton and ice-associated fauna. This is probably one of the most fundamental specialisations in polar bioproduction (Falk-Petersen et al. 1981; Clarke 1984; Hagen 1988) and a major reason for the biodiversity of indigenous populations of marine fish, mammals, and birds (Falk-Petersen 1988; Falk-Petersen et al. 1990). The stored lipids allow the animals to survive periods of food shortage and permit them to reproduce in a timely fashion. Their highly efficient lipid production usually takes place through the formation of wax esters and (or) triacylglycerols containing long-chain fatty acids and (or) fatty alcohols (Sargent and Henderson 1986; Kattner et al. 1996; Kattner and Hagen 1998). These high-energy compounds are biosynthesised by herbivorous zooplankton and rapidly transferred through the food chain to provide the caloric needs for higher trophic levels, including warm-blooded animals (Falk-Petersen et al. 1990). This lipid-derived flux of energy is likely to be a key determinant of biodiversity within polar systems.

Life cycles and lipid dynamics

There are clear differences in both spawning times and growth patterns as well as lipid levels and lipid compositions in the krill species investigated (Figs. 1 and 2; Tables 1 and 2). The lipid dynamics of the different species are linked closely to their life cycle strategies and enable the different species to utilise different ecological niches.

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Table 1. Life cycle characteristics of krill.

Species	Size (mm)	Longevity (years)	Spawning time	Dominant feeding type	Habitat
Arctic					
T. inermis	30	3–4	Onset of bloom	Herbivorous	Oceanic
T. raschii	30	3	Peak of bloom	Omnivorous	Neritic
T. longicaudata	20	2	During bloom	Carnivorous	Oceanic
M. norvegica	45	3	Not in arctic waters	Carnivorous	Neritic
Antarctic					
E. superba	60	4–6	After bloom	Omnivorous	Oceanic–cryopelagic
E. crystallorophias	41	4–5	Onset of bloom	Herbivorous–omnivorous	Neritic
T. macrura	37	3–4.5	Before bloom	Omnivorous	Oceanic

Note: Data from Einarsson (1945), Falk-Petersen and Hopkins (1981), Siegel (1987), and Dalpadado and Skjoldal (1996).

Thysanoessa inermis has a longevity of 3–4 years in Arctic waters. Spawning takes place just after the onset of the spring phytoplankton bloom on shelves and in fjords (Einarsson 1945; Dalpadado and Skjoldal 1996). In Balsfjorden, *T. inermis* spawns for the first time in its first year of life (Falk-Petersen and Hopkins 1981). The *T. inermis* 0-group grows rapidly during the spring bloom but shows little further growth through summer. At the end of this period (August), the total lipid accounts for 30% dry matter (DM), with phospholipids (55%) being the dominant lipid class (Falk-Petersen 1981; Falk-Petersen et al. 1981). After the autumn bloom, there is a new growth period when large amounts of lipid are elaborated (45% DM in October), mainly as wax esters. These lipid stores are mobilised during winter to sustain the animals and to fuel reproductive efforts. The lipid levels are reduced to nearly 10% DM, with the wax ester and triacylglycerol deposits reduced to zero (Falk-Petersen et al. 1982). In the animals' second year, there is a continuous elaboration of lipids during spring, summer, and autumn. Very high lipid levels (50 to nearly 60% DM) are recorded between August and February, with wax esters accounting for 45% and triacylglycerols for 20% of the lipid. These large energy stores, derived over the year from phytoplankton, are probably sufficient to sustain the animals over winter without food and also to fuel the development of gonads during late winter – spring. This suggestion is supported by fatty acid analyses, which suggest only a minor food intake by *T. inermis* during winter. From the above, we deduce that *T. inermis* has adapted to the seasonal changes in the food available by a propensity to convert its phytoplankton diet rapidly into lipids, mainly wax esters.

Thysanoessa raschii has a life span of 3 years and spawns at the culmination of the spring bloom (Falk-Petersen et al. 1981). At 70°N in Balsfjorden, spermatophore occurrence suggests that very few males breed in their first year but part of the female population does, while the whole adult population spawns in their second year of life (Falk-Petersen and Hopkins 1981). The first growth period in its first year lasts through May and June in Balsfjorden, followed by a period of no growth during summer and a second growth period during late autumn. During the first winter, 0-group *T. raschii* reaches nearly the same body length as *T. inermis* but only half the mass (Falk-Petersen 1985), and its lipid level is only 30% DM. The total lipid content remains low through the first winter with a further decrease in late winter – early spring. During the second summer, there is an increase in lipid level to 35–40% DM. Although *T. raschii* builds up lipid reserves, mainly as triacyglycerols during summer, the lipid stores are not large enough to carry the animals through the winter without dietary input.

Thysanoessa longicaudata is a purely oceanic species with a life span of 2 years that spawns in the spring and summer during or after the bloom (Einarsson 1945; Dalpadado and Skjoldal 1996; Astthorson and Gislason 1997). The species is found all over the Barents Sea and into the Spitsbergen fjords. The few lipid analyses available show moderate amounts of lipid, with triacyglycerols (maximum 51%) being the dominant neutral lipid class.

Meganyctiphanes norvegica has a life span of 3 years and does not spawn in Arctic waters. Its northern spawning limits are considered to coincide with the 5°C isotherm at 100 m, which coincides approximately with the Arctic Circle off the Norwegian coast (Einarsson 1945). Although *M. norvegica* cannot therefore be regarded as a truly Arctic species, it has been found in the Barents Sea (Drobysheva 1957) where it is likely that recruitment occurs from southern populations via the warm Norwegian Atlantic Current. During the animals' first winter, the lipid level reaches 40%, with the neutral lipids consisting only of triacyglycerols, which are mobilised during winter and spring to less than 20% in summer. During the second autumn, *M. norvegica* builds up large lipid stores as triacyglycerols (70% of total lipid). *Meganyctiphanes norvegica* is regarded as a carnivore, mainly preying on very lipid-rich calanoid copepods.

Euphausia superba is the predominant krill species in the Antarctic Ocean, with a biomass of hundreds of millions of tonnes. For a planktonic crustacean, it has an extremely long life cycle of 5–6 years (Siegel 1987). Reproduction can extend from mid-November to April with major spawning activities in January and February, especially at higher latitudes (Mauchline 1980; Quetin et al. 1994), later than *Euphausia crystallorophias* and *Thysanoessa macrura*. After a gonadal resting period during winter, oocyte development in *E. superba* occurs in spring and egg release in summer. Thus, reproductive processes are not fueled by lipid reserves during the winter period. The substantial amounts of energy required for gonad maturation and egg production are probably largely provided by ice biota during early spring and by phytoplankton blooms during late spring and summer. The concept is now widely accepted that in autumn, adult krill retreat under the advancing ice cover (Marschall 1988). However, the near depletion of lipid reserves suggests poor feeding conditions during the overwintering period and strong reliance on internal resources, at least in adults

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Table 2. Comparison of total lipid, triacylglycerols, and wax esters from different latitudes of Arctic krill species *T. inermis*, *T. raschii*, *T. longicaudata*, and *M. norvegica* and Antarctic species *E. superba*, *E. crystallorophias*, and *T. macrura*.

		Total lipid (% DM)				Triacylglycerol (% of total lipid)				Wax esters (% of total lipid)				
Species	Region	SU	AU	MAX	MIN	SU	AU	MAX	MIN	SU	AU	MAX	MIN	Reference(s)
T. inermis														
0-group	Balsfjorden (70°N)	25–30	30–45	50	12		8–10	10	8		18–20	40	0	Falk-Peteresen 1981
1-group		40–50	50–55	60	37	5–10	10–20	20	0	25–55	38–44	45	0	Falk-Petersen et al. 1981
2-group				45	38			20	0			60	0	Falk-Petersen et al. 1982
1-group	Kongsfjorden (79°N)	21				24	25			23	30			S. Falk-Petersen and J. Sargent, unpublished data
2-group		42												S. Falk-Petersen and J. Sargent, unpublished data
Adults	Fram Strait (75–80°N)	20–55	45–55	55	20									W. Hagen, unpublished data
T. raschii														
0-group	Balsfjorden (70°N)		25–30	30	25									Falk-Petersen 1981
1-group		35	34–36	42	35	38–40	42–54	54	0	5–10	10–12	30	0	Falk-Petersen et al. 1981
2-group				52	25			15	0			10	0	Falk-Petersen et al. 1982
1-group	Kongsfjorden (79°N)	20				31	37			8	12			S. Falk-Petersen and J. Sargent, unpublished data
T. longicaudata	Kongsfjorden (79°N)	25				32	51			8	9			S. Falk-Petersen and J. Sargent, unpublished data
Adults	Fram Strait (75–80°N)	25–40	40–55	55	20									W. Hagen, unpublished data
M. norvegica														
1-group	Balsfjorden (70°N)	28–33	40–42	48	22	35	45–55	70	22					Falk-Petersen 1981
Adults	Fram Strait (75–82°N)	20–50	18–44	56	13									W. Hagen, unpublished data
E. superba	Weddell Sea (68–77°S)	27	39	47	5	49		58	33					Hagen 1988; Hagen et al. 1996
E. crystallorophias	Weddell Sea (70–78°S)	35	44	52	6	5		10	2	47	56	61	14	Kattner and Hagen 1998
T. macrura	Weddell Sea (68–74°S)	39	47	57	5	2		4	1	62	67	70	39	Hagen and Kattner 1998

Note: SU, summer (July–August); AU, autumn (September–November); MAX, maximum lipid level, usually in winter; MIN, minimum lipid level, usually after spawning in spring.

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Table 3. Fatty acid and fatty alcohol compositions of triacylglycerols, wax esters, free fatty acids, and polar lipids from *T. inermis* sampled in Ullsfjorden and Balsfjorden, northern Norway (70°N).

					Wax esters								
	Triacylglycerols, acid				Acid				Alcohol				
Constituent	Jan.	Apr.	July	Nov.	Jan.	Apr.	July	Nov.	Jan.	Apr.	July	Free fatty acids (Nov.)	Polar lipids (Nov.)
14:0	9	3	4	4	2	1	1	1	29	12	16	0	1
16:0	33	29	30	29	6	4	5	4	52	51	54	10	23
16:1(*n*–7)	15	8	16	10	6	4	8	5	6	4	7	3	2
18:0	3	5	5	3	2	2	2	1				3	3
18:1(*n*–9)	7	10	8	9	54	59	51	51				10	7
18:1(*n*–7)	12	11	13	12	23	10	16	10				8	6
18:2(*n*–6)	2	3	2	2	2	2	1	1				1	2
18:3(*n*–3)	1	1	1	1		1	tr	1				1	2
18:4(*n*–3)	7	10	5	5	1	2	1	10				6	4
20:1(*n*–9)	1	1	1	4		2	1	10				5	2
20:5(*n*–3)	5	6	6	6	5	8	10	6				29	29
22:1(*n*–11)		1	1	5		1	10	7				7	2
22:6(*n*–3)		2	3	2		1	tr	tr				12	13
Phytol									10	23	19		
Sum PUFA	15	22		15	8	13	13	9				49	50

Note: tr, trace. Data from Sargent and Falk-Petersen (1981) and Sæther et al. (1986). Free fatty acid and polar lipid data are unpublished data from S. Falk-Petersen and J. Sargent.

(Quetin et al. 1994). In spring, the lipid levels of the adults reached minimum levels of 11% DM on average. Higher and more variable lipid contents occurred during summer, with 28% DM. In autumn, maximum lipid levels of 39% DM were found. These lipid reserves were mainly composed of triacyglycerols (e.g., Clarke 1980; Pond et al. 1995; Mayzaud et al. 1998), which made up about 50% of the total lipid during summer (Hagen 1988). In addition, phospholipids may also serve as storage lipids (Hagen et al. 1996), but the catabolism is still under discussion (Virtue et al. 1997). The dominance of triacyglycerols and the lack of wax esters have been taken as evidence for year-round feeding of *E. superba* (Clarke 1980; Sargent et al. 1981). A small percentage of individuals caught from around South Georgia in summer contained trace amounts of wax ester, which presumably reflects the occasional ingestion of copepods (Atkinson and Snyder 1997).

The "ice krill" *E. crystallorophias* is the most common euphausiid in high Antarctic neritic waters (e.g., John 1936). It feeds on phytoplankton in summer, but in contrast with *E. superba*, it has never been observed inhabiting ice crevices or scraping algae from the underside of the ice. It has a longevity of 4–5 years (Siegel 1987) and spawns in November–December (Harrington and Thomas 1987). Since in *E. crystallorophias*, spawning usually starts before the onset of phytoplankton production, it seems unlikely that this external resource contributes substantial amounts of energy during the final reproductive phase. The algal blooms will probably mainly be utilised to replenish the depleted lipid reserves of *E. crystallorophias* (Littlepage 1964). This is in accordance with the seasonal lipid pattern, which shows mean lipid levels of 35% DM in summer (February) and increases to 44% DM in autumn (April–May). The lowest levels are reached in late winter – early spring (October–November), before the onset of phytoplankton production, with significant differences between females (24% DM) and males (14% DM). Similarly, the major depot lipids in *E. crystallorophias*, wax esters (Bottino 1975), reach a maximum of almost 60% of total lipid in autumn but decrease in late winter – early spring to a minimum of 47% in females and 24% in males. The extensive lipid reserves accumulated in autumn by *E. crystallorophias* appear to be a prerequisite to provide energy for both survival during the food-limited dark season as well as sexual maturation and early spawning prior to the spring bloom. The early timing of reproduction has the advantage that the larval stages can make full use of the entire productive season in order to build up sufficient mass and energy depots to endure the winter.

Thysanoessa macrura has a rather oceanic distribution, similar to that of *E. superba*. It is an omnivorous species with a longevity of 4 years (Siegel 1987), and it may reach sexual maturity as early as after 13 months. Spawning starts in early September, before *E. crystallorophias*, and continues until November (e.g., Nordhausen 1994). Since reproduction in *T. macrura* commences well before the onset of primary production, this process is clearly independent of phytoplankton as an external energy source. This is supported by the total lipid data, which show a marked decrease from maximum levels of 47% DM in autumn to a minimum of 12% DM in early spring. The principal lipid composition of *T. macrura* is very similar to that of *E. crystallorophias*, with wax esters as primary depot lipids (Hagen and Kattner 1998). Maximum accumulation of wax esters occurred in autumn, about 67% of total lipid, whereas minimum levels (41%) were found in midwinter. The wide range of lipid contents in September (5–50% DM) and the steep lipid decline until November coincide with the intense reproductive activities of *T. macrura*. With respect to overwintering, lipid levels in August and early September in the Weddell Sea are typically still quite high and thus do not indicate a severe decrease in energy reserves during early and midwinter. No detailed information exists on its dietary preferences in winter,

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Table 4. Fatty acid and fatty alcohol compositions of triacylglycerols, wax esters, and polar lipids from *T. inermis*, *T. raschii*, and *T. longicaudata* sampled in Kongsfjorden, Svalbard (79°N).

	T. inermis						*T. raschii*						*T. longicaudata*					
	Triacylglycerols, acid		Wax esters		Polar lipids, acid		Triacylglycerols, acid		Wax esters		Polar lipids, acid		Triacylglycerols, acid		Wax esters		Polar lipids, acid	
Constituent	July	Sept.	Acid (July)	Alcohol (July)	July	Sept.	July	Sept.	Acid (July)	Alcohol (July)	July	Sept.	July	Sept.	Acid (July)	Alcohol (July)	July	Sept.
14:0	5	5	1	22	1	1	8	10	4	10	2	1	5	6	1	20	1	2
16:0	30	32	3	58	25	26	30	32	20	35	22	22	32	35	22	58	20	23
16:1(*n*–7)	30	21	14	14	6	6	23	15	45	11	4	5	12	18	41	15	4	7
C16 PUFA	4	4			1	1	1	2	tr		1	1	1	tr			tr	
18:0	2	3	1	tr	2	3	2	2	3	9	2	2	2	2	3	tr	2	1
18:1(*n*–9)	8	9	51	tr	6	7	15	16	4	1	8	7	22	19	16	tr	10	8
18:1(*n*–7)	13	12	15	tr	7	7	12	11	5	2	8	9	11	9	6	tr	5	5
18:2(*n*–6)	1	1	1		1	1	1	1	tr		1	1	1	1			2	2
18:3(*n*–3)	tr	1	tr		1	1	tr	1			1	1	tr	tr			1	1
18:4(*n*–3)	2	5	tr		4	6	1	2	tr		3	3	tr	tr			1	1
20:1(*n*–9)	1	1	2	2	tr	tr	1	1	1	9	1	1	5	3		2	1	2
20:1(*n*–7)					tr	tr					1	1					tr	tr
20:4(*n*–6)					1	1					1	1					1	1
20:4(*n*–3)					tr	1					tr	1					1	1
20:5(*n*–3)	3	3	4	0	30	29	2	2	3	0	26	28	1	1	1	0	28	27
22:1(*n*–11)	1	tr	1	2	tr	tr	tr	1	1	7	tr	1	5	2	6	3	1	1
22:1(*n*–9)		tr			tr	tr		tr			tr	tr		1			tr	1
22:5(*n*–6)					tr	tr					tr	tr					tr	tr
22:5(*n*–3)					tr	tr					1	1					1	1
22:6(*n*–3)	tr	1	tr		11	10	1	1	tr		16	13	1	1	1		20	16
Phytol										tr								
Sum PUFA	10	15	5		51	49	6	9	4		49	49	5	4	2		55	49

Note: tr, trace. Unpublished data from S. Falk-Petersen and J. Sargent.

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Table 5. Fatty acid and fatty alcohol compositions of triacylglycerols, wax esters, free fatty acids, and polar lipids from *T. raschii* sampled in Ullsfjorden and Balsfjorden, northern Norway (70°N).

						Wax esters									
	Triacylglycerols, acid					Acid				Alcohol					
Constituent	Jan.	Feb.	Apr.	July	Nov.	Jan.	Apr.	July	Nov.	Jan.	Apr.	July	Nov.	Free fatty acids (Nov.)	Polar lipids (Nov.)
14:0	14	9	3	5	8	5	1	2	1	2	5	2	8	2	1
16:0	31	30	23	30	29	35	8	10	6	2	30	27	29	12	20
16:1(*n*–7)	12	8	7	14	10	8	3	8	4		2	3	3	4	2
18:0	2	9	4	4	2	6	3	3	1					3	2
18:1(*n*–9)	12	14	16	16	13	9	46	39	41					7	6
18:1(*n*–7)	11	8	10	12	10	11	11	15	10				11	6	6
18:2(*n*–6)	2	2	3	1	1	1	2	1	1					1	2
18:3(*n*–3)	1	1	1	1	1		1	1	1					1	2
18:4(*n*–3)	2	3	9	3	3	1	3	1	1					6	3
20:1(*n*–9)	1		3	1	3	4	2	1	12				10	3	2
20:5(*n*–3)	4	5	8	5	6	7	10	11	6					22	30
22:1(*n*–11)	1	2	2	1	4	3	2	1	12				24	5	2
22:6(*n*–3)	1	1	3	1	1		1	1	tr					6	14
Phytol										93	52	64	20		
Sum PUFA	8	11	23	11	11	9	18	14	9					36	52

Note: tr, trace. Data from Sargent and Falk-Petersen (1981) and Sæther et al. (1986). Free fatty acid and polar lipid data are unpublished data from S. Falk-Petersen and J. Sargent.

but during late summer and early autumn, there is a clear tendency towards carnivorous feeding (Hopkins 1985; Hopkins and Torres 1989). However, the exploitation of alternative food sources such as zooplankton can apparently not compensate for the lack of phytoplankton during the dark season to provide sufficient energy for reproduction.

Trophic relationships and lipid biomarkers

The food pathways in the pelagic and ice-associated marine ecosystems originate in growing phytoplankton and ice algae whose organic constituents are ingested and transformed by animals up the food chain. Actively growing algae contain in the region of 10–20% DM as lipids, of which approximately 50% are (*n*–3) polyunsaturated fatty acids (PUFA). Lipid levels increase from 10–20% in phytoplankton to 50–70% in herbivorous animals, including the krill species studied here. This increase in lipid levels, combined with a high assimilation efficiency of key components of the polar marine food chain, is one of the most the fundamental and key specialisations in pelagic polar ecosystems.

The use of fatty acids as biomarkers is based on studies of the lipid composition of marine algae, which show that the fatty acid compositions are characteristic of the different taxa (Sargent and Whittle 1981; Volkmann et al. 1989; Dunstan et al. 1992). Of the important phytoplankton in polar waters, the diatoms tend to be rich in 20:5(*n*–3), 16:1(*n*–7), and C16 PUFA but deficient in C18 PUFA. The dinoflagellates tend to be rich in 18:4(*n*–3), 18:5(*n*–3), and especially 22:6(*n*–3) and deficient in 16:1(*n*–7). The Haptophyceae *Phaeocystis pouchetii* that often dominates the blooms in polar waters (Falk-Petersen and Hopkins 1981; Verity and Smetacek 1996) is rich in C18 PUFA, especially 18:4(*n*–3) and 18:5(*n*–3), together with 20:5(*n*–3) and 22:6(*n*–3), while 16:1(*n*–7) is found in very small amounts (Sargent et al. 1985; Hamm et al. 2000).

Table 6. Fatty acid and fatty alcohol compositions of triacylglycerols, free fatty acids, and polar lipids from *M. norvegica* sampled in Ullsfjorden and Balsfjorden, northern Norway (70°N).

	Triacylglycerols, acid			
Constituent	Jan.	Apr.	Free fatty acids (Nov.)	Polar lipids (Nov.)
14:0	8	7	8	1
16:0	19	10	17	15
16:1(*n*–7)	5	4	4	2
18:0	1	1	2	1
18:1(*n*–9)	14	10	11	13
18:1(*n*–7)	7	3	6	4
18:2(*n*–6)	1	1	2	2
18:3(*n*–3)	1	1	2	2
18:4(*n*–3)	2	1	2	tr
20:1(*n*–9)	12	21	9	6
20:5(*n*–3)	7	3	12	16
22:1(*n*–11)	6	26	8	4
22:6(*n*–3)	6	4	11	27
Phytol				
Sum PUFA	17	11	28	47

Note: tr, trace. Data from Sargent and Falk-Petersen (1981) and Sæther et al. (1986). Free fatty acid and polar lipid are unpublished data from S. Falk-Petersen and J. Sargent.

The above findings can be related to the detailed fatty acid and alcohol compositions of various krill species (Sargent and Falk-Petersen 1981; Kattner et al. 1996; Cripps et al. 1999). Oleic acid, 18:1(*n*–9), is a major fatty acid of most marine animal lipids. The 18:1(*n*–7) unit is also frequently

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Table 7. Fatty acid and fatty alcohol compositions of triacylglycerols and polar lipids from *E. superba* sampled in the Weddell Sea (70–76°S).

	Triacylglycerols		Polar lipids	
Constituent	Jan.	Apr.	Jan	Apr.
14:0	19	20	5	7
16:0	25	22	21	18
16:1(*n*–7)	9	7	2	3
C16 PUFA	2	3		
18:0	3	2	3	1
18:1(*n*–9)	26	24	9	11
18:1(*n*–7)	5	7	6	8
18:2(*n*–6)	2	3	2	3
18:3(*n*–3)	1	1	1	1
18:4(*n*–3)	4	5	5	6
20:1(*n*–9)	2	1	1	1
20:1(*n*–7)				
20:4(*n*–6)			1	1
20:4(*n*–3)				
20:5(*n*–3)	1	2	26	21
22:1(*n*–11)			1	
22:1(*n*–9)			1	
22:5(*n*–6)		tr		1
22:5(*n*–3)	1	3	18	20
22:6(*n*–3)	10	15	54	52
Phytol				
Sum PUFA	10	15	54	52

Note: tr, trace. Unpublished data from W. Hagen and G. Kattner.

found in large quantities deriving from the elongation of 16:1(*n*–7) that is likely to originate substantially from phytoplankton. This means that 16:1(*n*–7) and 18:1(*n*–7) in animal lipids tend to reflect phytoplanktonic dietary input, whereas 18:1(*n*–9) reflects animal dietary input. The 20:1(*n*–9) and 22:1(*n*–11) units, present in very large amounts in calanoid copepods, are considered to be formed by de novo biosynthesis in these animals, which in our present understanding are the major site of the formation of 20:1(*n*–9) and 22:1(*n*–11) units in the marine food web (Sargent and Whittle 1981; Kattner and Hagen 1995).

Thysanoessa inermis stores large lipid reserves as adults (55% DM) during autumn, mainly as wax esters. Considerations of fatty acid and alcohol compositions (Table 3) together with the high wax ester level suggest a phytoplanktonic diet. In Balsfjorden–Ullsfjorden, the high level of C18 PUFA in the triacylglycerols and of 20:5(*n*–3) in both triacylglycerols and wax esters probably derive directly from phytoplankton. The level of 18:4(*n*–3), so abundant in *P. pouchetii*, also indicates that this alga is an important part of the diet. Hamm et al. (2000), using fatty acid and sterol biomarkers, found that *T. inermis* in Balsfjorden grazed efficiently on *Phaeocystis* colonies and that *Phaeocystis* was the major food source of this species during spring. Moderate to high levels of phytol (23% in April) also indicate substantial input of decaying plant material, especially during spring. Increased amounts of 20:1(*n*–9) and 22:1(*n*–11) in November point to greater *Calanus* dietary inputs during winter. In Kongsfjorden, the low 18:1(*n*–7)/18:1(*n*–9) ratio in the wax ester acid indicates that a mixed animal dietary input can be an important part of the food in this high-latitude fjord. There are no signs of phytol, which could indicate ingestion of detritus of phytoplanktonic origin or that *Calanus* is a part of the diet of *T. inermis* in Kongsfjorden (Table 4).

Thysanoessa raschii adults also build up considerable stores of lipids (40–45% DM) during summer and autumn, consisting mainly of triacyglycerols. The high levels of 14:0 and 18:1(*n*–7) in the triacyglycerols (Table 5) are consistent with a significant dietary input of phytoplankton. However, the levels of 20:5(*n*–3) and 18:4(*n*–3) are much higher in spring (April) than in winter in Balsfjorden–Ullsfjorden. This might indicate a dietary shift from a phytoplanktonic diet in summer to a more omnivorous diet in winter. The latter is supported by the accumulation of large amounts of phytol during January (Falk-Petersen et al. 1981). This input can only originate from detrital feeding on bottom sediments or from abundant nonliving particulate material of phytoplanktonic origin in the water column (Sargent and Falk-Petersen 1981). Significant amounts of 20:1(*n*–9) and 22:1(*n*–11) moieties in the wax esters in November also point to a small but significant intake of food of *Calanus* origin. The omnivorous nature of *T. raschii* can also be seen in Kongsfjorden. Low 18:1(*n*–7)/18:1(*n*–9) ratios and significant amounts of 22:1(*n*–11) indicate an animal dietary intake, while high levels of 16:1(*n*–7) in July show an input of large amounts of diatoms in spring–summer (Table 4). In contrast with the Balsfjorden–Ullsfjorden fjord complex, the very low levels of phytol in the animals in Kongsfjorden point to a fundamental difference between the two systems, namely that detrital or nonliving particulate material of phytoplankton origin is not present or is not available as food in Kongsfjorden.

Thysanoessa longicaudata has triacyglycerols as its major neutral lipid class. The very low 18:1(*n*–7)/18:1(*n*–9) ratios (<0.6) and significant amounts of 20:1(*n*–9) and 22:1(*n*–11) moieties indicate animal dietary input, with *Calanus* being an important part of the food (Table 4). The nearly complete absence of C18 PUFA, 20:5(*n*–3), and 22:6(*n*–3) in the triacyglycerols shows that neither diatoms, dinoflagellates, nor *Phaeocystis* are part of the diet.

Meganyctiphanes norvegica builds up substantial amounts of lipids (nearly 50% of the DM) as triacyglycerols during autumn. The relative deficiency of 16:1(*n*–7), C18 PUFA, 20:5(*n*–3), and 22:6(*n*–3) in the triacyglycerols indicates a relatively small input of phytoplanktonic lipid. The very low 18:1(*n*–7)/18:1(*n*–9) ratio (0.3–0.5) together with high amounts of 20:1(*n*–9) and 22:1(*n*–11) fatty acids, especially in April, is also consistent with a large dietary input of 20:1(*n*–9) and 22:1(*n*–11) fatty acids and alcohols from calanoid copepod wax esters during the spring bloom (Table 6).

In *E. superba*, the predominant depot lipids are triacyglycerols. They are mainly composed of the fatty acids 14:0, 16:0, and 18:1(*n*–9) (Table 7). The next abundant fatty acids, the typical phytoplankton markers 16:1(*n*–7) and 18:4(*n*–3) as well as 18:1(*n*–7), suggest that *E. superba* feeds mainly on phytoplankton. This is also confirmed by hydrocarbon analyses (Cripps and Hill 1998). Although *E. superba* is known to take copepods on occasion (Atkinson and Snyder 1997; Cripps et al. 1999), from the near absence of lipid components such as 20:1 and 22:1 fatty acids and alcohols, it can be concluded that the prevailing calanoid copepods

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Table 8. Fatty acid and fatty alcohol compositions of triacylglycerols, wax esters, and polar lipids from *E. crystallorophias* sampled in the Weddell Sea (70–77°S).

	Triacylglycerols					Wax esters				Polar lipids, acid	
	Acid										
Constituent	Nov.	Jan.	Apr.	Acid (Nov.)	Alcohol (Nov.)	Acid (Jan.)	Alcohol (Jan.)	Acid (Apr.)	Alcohol (Apr.)	Nov.	Apr.
14:0	4	17	6	0	71	1	10	0	65	3	3
16:0	25	22	17	0	28	5	11	1	32	21	23
16:1(*n*–7)	2	14	14	6	1	6	1	8	1	4	6
16:2		3				1	0				
16:3		1				tr	0				
16:4		3				tr	0				
C16 PUFA			2					0			0
18:0	5	2	2			3	1			1	1
18:1(*n*–9)	40	19	24	75		17	2	64		20	14
18:1(*n*–7)	13	6	7	16		19	1	20		8	5
18:2(*n*–6)	2	2	1	2		3	1	1		2	1
18:3(*n*–3)		1	1			1	0	1		1	1
18:4(*n*–3)		4	5	0		3	0	2			3
20:1(*n*–9)	1	1	1	1		5	9	2	2		1
20:4(*n*–6)	1		0							1	1
20:5(*n*–3)	4	4	12	0		26	0	1		23	26
22:1(*n*–11)		tr	0			2	3		0		0
22:1(*n*–9)		tr				0	1				
22:5(*n*–3)		tr				1	0				
22:6(*n*–3)	2	1	7	0		3	0	0		17	16
Phytol							52				
Sum PUFA	9		28	2				5		44	48

Note: tr, trace. Selected data from Kattner and Hagen (1998) and Falk-Petersen et al. (1999).

Calanoides acutus and *Calanus propinquus* are not important food items overall for *E. superba*.

Euphausia crystallorophias biosynthesises wax esters as major storage lipid with short-chain alcohol moieties (Table 8). The fatty acids are generally predominated by 18:1, mainly consisting of the (*n*–9) isomer, which reflects omnivorous or even carnivorous feeding. On the other hand, the significant 18:1(*n*–7) fraction abundant in the triacylglycerols indicates phytoplankton uptake. The other typical trophic marker fatty acid, 18:4(*n*–3), is also mainly found in the triacylglycerols (Kattner and Hagen 1998), which are more immediate indicators of dietary influences than wax esters. Falk-Petersen et al. (1999), sampling small specimens of *E. crystallorophias* under an ice floe in a prebloom situation, found a very different composition. Large amounts of phytol and the 20:5(*n*–3) fatty acid in the wax esters indicate that *E. crystallorophias* may consume detrital material derived from ice algae associated with the ice floes before the onset of the bloom.

In *T. macrura*, wax esters are also the prevailing lipid class. However, as compared with *E. crystallorophias*, the dominance of the 18:1 alcohols in *T. macrura* (Table 9) is strikingly different (Kattner et al. 1996). Although they may be biosynthesised de novo, the high amounts of the 18:1(*n*–9) alcohol could also reflect carnivorous feeding, since they originate from the 18:1(*n*–9) fatty acid, a typical component of metazoans. The high concentration of the 20:1(*n*–9) alcohol in the lipids of *T. macrura* may be explained by the ingestion of the abundant *C. acutus*, the only known Antarctic copepod with substantial amounts of this alcohol (Hagen et al. 1993; Kattner et al. 1994). On the other hand, the abundant 18:1(*n*–7) reflects phytoplankton ingestion, as discussed for *E. crystallorophias*. The 16:1(*n*–7) and 18:4(*n*–3) fatty acids are only minor components in the *T. macrura* lipids without seasonal variations. In autumn, the high amounts of the 18:4(*n*–3) fatty acid in furciliae of *T. macrura* suggest a dependence on phytoplankton such as flagellate species by these early developmental stages (Hagen and Kattner 1998). In contrast, there is no clear trophic signal in the fatty acid compositions of adult *T. macrura*. The other trophic marker fatty acid, 16:1(*n*–7), is only a minor component in the *T. macrura* lipids and exhibits no seasonal variability. Since this euphausiid is known to also feed on phytoplankton (Hopkins 1985, 1987), we suggest that both fatty acids are ingested with the diet and either catabolised or modified.

Biosynthesis of lipids

Since all of these krill species are able to accumulate large amounts of lipids during periods of plentiful food, high rates of lipid biosynthesis must be achieved. Except for *E. superba* and *M. norvegica*, all krill species studied here are able to synthesise wax esters. Both wax esters and triacyglycerols are stored as major depot lipids by the various krill species. These lipid classes as well as phospholipids

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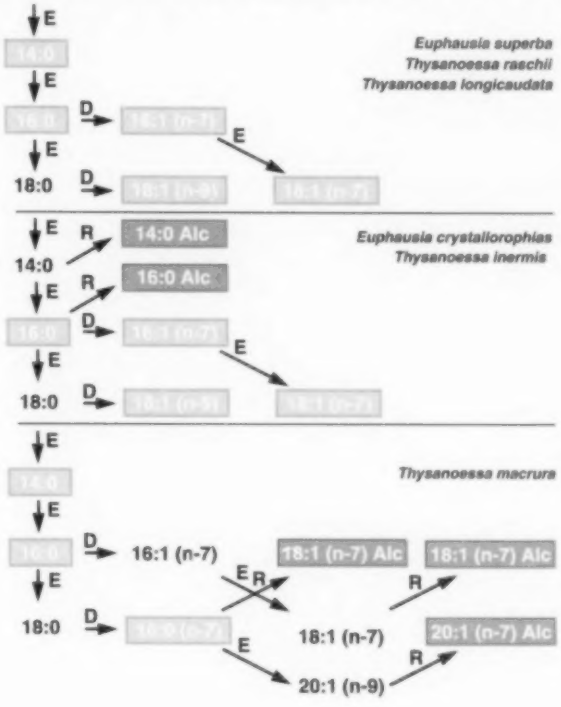
Table 9. Fatty acid and fatty alcohol compositions of wax esters and polar lipids from *T. macrura* sampled in the Weddell Sea (68–71°S).

	Wax esters				
Constituent	Acid (Jan.)	Alcohol (Jan.)	Acid (Apr.)	Alcohol (Apr.)	Polar lipids, acid (Apr.)
14:0	35	1	38		4
16:0	25	1	26		18
16:1(*n*–7)	7	tr	6		4
C16 PUFA	1		2		
18:0	2	1	1		1
18:1(*n*–9)	12	36	17	42	13
18:1(*n*–7)	4	31	5	42	4
18:2(*n*–6)	1	tr	1		2
18:3(*n*–3)		1			
18:4(*n*–3)					1
20:1(*n*–9)	2	19		12	
20:1(*n*–7)					
20:4(*n*–6)					2
20:4(*n*–3)					1
20:5(*n*–3)	10		2		26
22:1(*n*–11)		1		5	1
22:1(*n*–9)		1	1		1
22:5(*n*–6)					
22:5(*n*–3)					1
22:6(*n*–3)					22
Phytol					
Sum PUFA	12	1	5		55

Note: tr, trace. Selected data from Hagen and Kattner (1998).

Fig. 3. Biosynthetic pathways of fatty acids and fatty alcohols in polar krill species with special regard to the major neutral lipid classes. E, elongation; D, desaturation; R, fatty acid reduction to alcohol (Alc); shaded boxes, dominant fatty acids and alcohols.



need fatty acids as basic constituents. All species seem to have the capacity to biosynthesise fatty acids de novo by conventional mechanisms, although extensive de novo synthesis is unusual in animals when large amounts of dietary lipids are ingested. For the biosynthesis of wax esters, fatty acids have to be converted into fatty alcohols by fatty acyl coenzyme A reductase. Therefore, high levels of fatty alcohols require abundant sources of fatty acid substrates in the animal.

One possible mechanism of lipid production is the de novo biosynthesis in the animal by type I fatty acid synthetase. The 18:0 and 16:0 moieties are the major end products, which may be converted by delta-9 fatty acid desaturase to 18:1(*n*–9) and 16:1(*n*–7), respectively, with 16:1(*n*–7) subsequently being chain-elongated to 18:1(*n*–7) (Fig. 3). Secondly, fatty acids and alcohols could be formed by the elongation and, if necessary, delta-9 desaturation of a range of shorter-chain saturated and monounsaturated fatty acids, particularly 14:0, 16:0, and 16:1(*n*–7), derived from the animals diet. The 16:1(*n*–7) fatty acid that is abundant in phytoplanktonic lipid, particularly in diatoms, is the obvious precursor of the 18:1(*n*–7) fatty acid and alcohol, which are especially abundant in *T. macrura* as alcohol (Kattner et al. 1996) and a common fatty acid in all krill species. The general combinations in the wax esters are shorter-chain fatty alcohols (14:0 and 16:0) with fatty acids of 16 and 18 carbon atoms, the latter as monounsaturates. The only exception is *T. macrura* where this scheme is reversed, i.e., its wax esters are a combination of 18:1 alcohols and shorter-chain fatty acids (Fig. 3). The capability to produce wax esters with very long-chain fatty acids and alcohols seems not to be present in krill species, which is in contrast with calanoid copepods (Kattner and Hagen 1995). Thus, the energy demand and the necessity to produce high energy-lipids are less pronounced in the krill species.

It has been suggested (Sargent and Henderson 1986) that the formation of fatty alcohols in the elaboration of wax esters is a mechanism for removing end-product inhibition in fatty acid biosynthesis while producing a more reduced, i.e., more energy-rich, final end product. Therefore, the formation of wax esters accelerates de novo biosynthesis of lipids in the presence of abundant dietary lipids.

Functions of lipids in krill

Neutral lipid reserves are accumulated by krill, and indeed by all animals, whether marine or terrestrial, fundamentally as metabolic energy reserves for future use. However, neutral lipids in krill, and indeed in marine animals generally, have also been implicated in buoyancy regulating mechanisms. There are two aspects to this, the first being the inverse relationship between the lipid level and the water content of krill as determined by Falk-Petersen (1985). Krill catabolise lipid to generate energy during late winter and early spring and accumulate lipid during the following sum-

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mer and autumn. Lipid is mobilised to generate free fatty acids that are combusted by the process of beta-oxidation, yielding carbon dioxide and water and generating metabolic energy in the form of ATP. The stoichiometry of fatty acid beta-oxidation is such that during the complete oxidation of a fatty acid to carbon dioxide and water, one volume of fatty acid generates an equal volume of water. Thus, an inverse relationship exists between fat and water. Such a relationship is well established for fish (e.g., Henderson et al. 1984). It ensures that the body volume of the fish does not change during periods of extensive lipid oxidation that occur during oogenesis, such that the buoyancy of the fish is maintained. This process of maintaining body volume by replacing fat with water during times of excessive fat oxidation can account well for the findings of Falk-Petersen (1985) implying that krill exploit the inverse relationship between fat and water to regulate buoyancy.

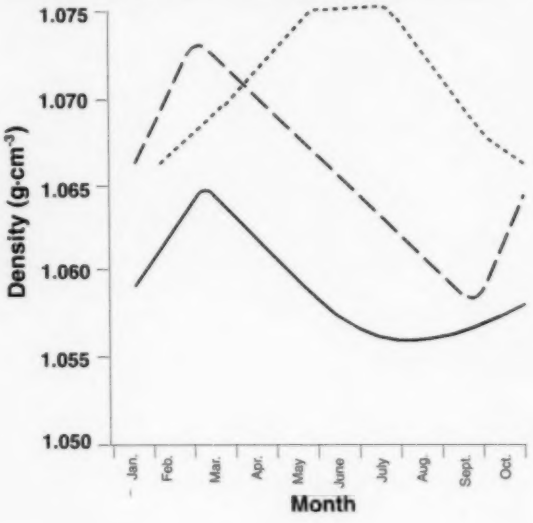
The second aspect of lipids being involved in buoyancy regulation stems from all neutral lipids having a specific gravity less than that of water so that they generate upthrust in water. The advantage of lipids as buoyancy aids (Clarke et al. 1984) is of fundamental importance in pelagic species such as polar copepods and krill. With a specific gravity of seawater of 1.026 $g \cdot cm^{-3}$, pure wax esters of 0.86 $g \cdot cm^{-3}$ and triacyglycerols of 0.93 $g \cdot cm^{-3}$ generate considerable upthrust. Variations in the density of euphausiids are closely related to the lipid level and lipid composition. Since the amounts of wax esters and total lipid are higher in *T. inermis* than in *T. raschii*, it is not surprising that *T. inermis* has a lower density than *T. raschii* (Fig. 4). The density decrease in *T. inermis* from approximately 1.065 $g \cdot cm^{-3}$ in March to 1.055 $g \cdot cm^{-3}$ in July and in *M. norvegica* from 1.075 $g \cdot cm^{-3}$ in May to 1.065 $g \cdot cm^{-3}$ in October is also closely related to the lipid level and reflects the different lipid dynamics in these species.

Comparison of the Arctic and Antarctic

Polar oceans in the Northern and Southern hemispheres are characterised by extreme seasonal oscillations in incident radiation and variations in ice cover on a wide range of time scales. The most important factor influencing polar euphausiids is the phytoplankton bloom, which can vary markedly in intensity and duration between years. This influences the structure of polar marine ecosystems, resulting in lower biodiversity but higher abundances and shorter food chains in the pelagic ecosystem. Pelagic euphausiids are among the most numerous species in polar oceans, and they provide a valuable example of the diversity of ecological lifestyles in relation to the variability of polar marine systems (Figs. 1 and 2). Based on their life cycle strategy and ecological niche, the various krill species can be characterised as predominantly herbivorous, omnivorous, or carnivorous.

The Arctic *T. inermis* and the Antarctic *E. crystallorophias* can be classified as high polar hebivores. They start spawning before the onset of the spring bloom and their reproductive processes are fueled mainly by lipid reserves synthesised during the previous year. They reach a similar adult size, with a longevity of 3–5 years, and both synthesise large lipid

Fig. 4. Seasonal variation in density of adult 20-mm *T. inermis* (solid line), 20-mm *T. raschii* (short-dashed line), and 35-mm *M. norvegica* (long-dashed line). After Køgeler et al. (1987).



reserves, mainly as wax esters, during spring and summer. The lipid reserves are large enough to sustain them through the winter with little or no food supply, although most of the lipid deposits are utilised for reproductive processes. The fatty acid and alcohol compositions together with the high wax ester levels suggest a phytoplanktonic diet and an uptake of decaying material of phytoplanktonic origin in winter – early spring. It has been suggested that in Antarctic waters, *E. crystallorophias* consumes detrital material derived from ice floes (Sargent and Falk-Petersen 1981; Falk-Petersen et al. 1999). In Arctic waters, *T. inermis* ingests detritus from the bottom sediments, and in both species, this goes some way to meet dietary requirements during winter. Both *T. inermis* and *E. crystallorophias* can thus be classified as high-latitude herbivores, adapted to exploit the typical high-latitude bloom situation; both species, however, can supplement their dietary requirements during winter by utilising decaying material of phytoplanktonic origin.

The Antarctic *T. macrura* is a midlatitude open-water omnivore. It spawns well before the bloom and its reproduction must therefore be independent of the spring–summer phytoplankton bloom as an external food source. Its longevity and size are the same as those of *T. inermis*, *T. raschii*, and *E. crystallorophias*. It synthesises large lipid reserves during late summer and autumn, mainly as wax esters. *Thysanoessa macrura* exhibits lipid dynamics similar to those of *T. inermis*, retaining its lipids and wax ester reserves during winter and preferentially mobilising the wax ester as fuel for reproductive processes (Hagen and Kattner 1998). The fatty acid and fatty alcohol compositions of *T. macrura* are strikingly different from those of other zooplankton species, particularly the high level of 18:1(*n*–9) and 18:1(*n*–7) alcohols, which are rare in other marine zooplankton species (Kattner et al. 1996). The depot lipids of *T. macrura* are low in fatty acids characteristic of diatoms

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and flagellates. Together with its lipid dynamics, this suggests that *T. macrura* is an omnivore with a dietary input much more diverse than that found in the classical spring bloom situation.

The Arctic *T. raschii* and Antarctic *E. superba* are omnivores feeding for large periods of the year. They spawn during or just after the spring bloom, respectively, and dietary inputs from phytoplankton are essential for sexual maturation and spawning (Falk-Petersen and Hopkins 1981; Hagen et al. 1996). Both species build up high levels of lipids, mainly as triacylglycerols, but these reserves are not large enough to both sustain the animals through the winter and fuel their reproductive processes. In northern Norwegian fjords, the large increase in phytol during late winter in *T. raschii* can only originate from detrital feeding on nonliving particulate material of phytoplanktonic origin (Sargent and Falk-Petersen 1981). Significant amounts of lipid moieties of calanoid origin and low 18:1(*n*–7)/18:1(*n*–9) ratios during winter also point to carnivory in *T. raschii* in Arctic waters. *Thysanoessa raschii* and *E. superba* can therefore be classified as typical omnivores, feeding on algae but also ingesting decaying detritus of phytoplanktonic origin as well as metazoans during winter.

A striking difference between the Arctic and the Antarctic is the presence of two carnivorous species in Arctic waters, the North Atlantic expatriate *M. norvegica* and the oceanic *T. longicaudata*. *Meganyctiphanes norvegica* is a large and robust species, while *T. longicaudata* is the smallest euphausiid studied here. Both species have only small amounts of 16:1(*n*–7), C18 PUFA, 20:5(*n*–3), and 22:6(*n*–3) in their triacyglycerols, indicating a relatively small input of phytoplanktonic lipid, while the very low 18:1(*n*–7)/18:1(*n*–9) ratio (0.3–0.5) together with high amounts of 20:1(*n*–9) and 22:1(*n*–11) suggests a substantial dietary input of calanoid copepods and (or) other animals.

From the above considerations and our knowledge of the life cycles, lipid dynamics, and biosynthetic pathways, we may conclude the following. (*i*) *Thysanoessa inermis* and *E. crystallorophias* are the only species from a true polar habitat, able to utilise and survive mainly on the yearly phytoplankton bloom. Both species accumulate large lipid deposits, mainly as wax esters, that are utilised primarily for reproductive processes. While *T. inermis* is largely herbivorous, *E. crystallorophias* tends to a herbivorous–omnivorous feeding mode. (*ii*) *Thysanoessa raschii*, *T. macrura*, and *E. superba* are much more boreal and appear to require feeding to survive overwinter (although *E. superba* has been reported to utilise degrowth in the laboratory, this has yet to be reliably reported from the wild). *Thysanoessa macrura* shows some similarities to the Arctic *T. inermis* in its very high lipid and wax ester levels. *Thysanoessa macrura* also spawns well before the bloom and its reproduction is independent of the bloom as an external food source. *Thysanoessa raschii* and *E. superba* show a less pronounced lipid storage, mainly as triacyglycerols, and apart from lipid reserves, they rely on detritus and ice algae, respectively, for overwintering and are dependent on dietary input from the spring bloom to reproduce. (*iii*) *Thysanoessa longicaudata* is a North Atlantic polar carnivore utilising *Calanus* as its main food source, similar to the major pelagic fish stocks (capelin and herring) in the area, while the triacylglycerol-storing *M. norvegica* is an expatriate carnivore in Arctic shelf waters with its main distribution centred further south.

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Behavior of Antarctic krill (*Euphausia superba*): schooling, foraging, and antipredatory behavior

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Abstract: Aspects of the behavior of pelagic euphausiids are reviewed, emphasizing the behavioral biology of Antarctic krill (*Euphausia superba*). *Euphausia superba* makes an abrupt behavioral transition after the last larval molt from an individualistic, planktonic lifestyle to that of a highly social, nektonic juvenile. Then and throughout the rest of its life, most aspects of krill behavior are expressed within the context of highly organized, polarized schools. A krill school is an integrated whole that displays properties greater than the sum of its parts. Emergent attributes of the aggregate evolve in response to a suite of positive and negative selective factors that act on entire schools as well as individuals. We evaluate the individual advantages and disadvantages of living within large schools of conspecific euphausiids primarily for foraging, antipredator behavior, and epidemiology. We review the history of research on krill behavior, comment on the current state of knowledge, and suggest new avenues for future investigations.

Résumé : On trouvera ici une revue de certains aspects de l'éthologie des euphausiidés pélagiques, en particulier de la biologie comportementale du krill antarctique (*Euphausia superba*). Après sa dernière mue larvaire, *Euphausia superba* troque abruptement son mode de vie planctonique et individualiste pour une vie juvénile nectonique et hautement sociale. À partir de ce moment et pour le reste de sa vie, le krill a un comportement qui s'exprime presque toujours dans le contexte de bancs très organisés et polarisés. Un banc de krill forme un tout intégré dont les propriétés collectives dépassent la somme des propriétés individuelles. Les attitudes collectives apparaissent et évoluent en réaction à une séquence de facteurs sélectifs positifs et négatifs qui agissent tant sur le banc que sur les individus. Nous évaluons les avantages et les inconvénients pour un individu de vivre à l'intérieur de grands bancs monospécifiques d'euphausiidés, surtout en ce qui a trait à la quête de nourriture, au comportement antiprédateur et à l'épidémiologie. Nous passons en revue les études antérieures sur le comportement du krill, évaluons les connaissances actuelles et suggérons de nouvelles perspectives de recherche.

[Traduit par la Rédaction]

Introduction

The Antarctic krill (*Euphausia superba*) is of central importance in the Antarctic ecosystem. According to Hopkins (1985), in Croker Passage, Antarctica, "*Euphausia superba* (17–52 mm) dominated the pelagic biomass, exceeding zooplankton standing stock under a square meter of ocean by a factor of 15." Throughout much of its life, *E. superba* occurs within 100 m of the surface in discrete schools (e.g., Marr 1962; Hamner et al. 1983; Watkins et al. 1986). Reddish patches of krill are often visible at the surface, and gross attributes of krill aggegrations, such as shape, size, and density, have been appreciated for 60 years (e.g., Hardy and Gunther 1935; Nemoto 1983; Miller and Hampton 1989). Nonetheless, the first underwater observation of krill schools at sea was made only 30 years ago (Ragulin 1969), *E. superba* has been maintained in laboratory aquaria for only 20 years (McWhinnie and Denys 1980), and we have begun to learn about the complex behavior of krill only recently (Hamner et al. 1983; O'Brien 1987*b*; Ritz 1994).

Our research on the behavior of *E. superba* has emphasized underwater observations of krill via use of bluewater scuba diving techniques in Antarctic waters (Hamner 1982), but we have also conducted extensive aquarium studies at Palmer Station, Antarctica, and aboard ship (e.g., Hamner et al. 1983; Stretch et al. 1988; Strand and Hamner 1990). Our most important qualitative contribution to krill biology was confirmation that krill are obligate schoolers, the Antarctic ecological equivalent of temperate zone, schooling clupeid fishes.

Our initial observations of schooling krill in Antarctic waters occurred when we were surrounded by hundreds of thousands of animals under ideal conditions (Hamner 1984*b*), but in situ research in the Antarctic was frustrating because krill schools and good diving weather did not always coincide. With experience and increased knowledge of seabird behavior, our success in finding krill in calm seas increased dramatically, but underwater visibility was often poor (Hamner 1984*b*, photo on p. 642), and krill schools located acoustically frequently were far below scuba depth limits. Furthermore, krill, like sardines, form dense schools, and individuals within a krill school are difficult to track due to visual confusion generated by the group as a whole (photographs by F. Nicklin in Hamner 1984*a*, 1984*b*). Thus, in comparison with other ethological investigations where focal observations are counted in thousands of hours, we have had

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only a brief and inadequate glance at the complex behavioral repertoire of krill.

Knowledge about behavior of oceanic animals is critical for understanding marine ecosystems, but apparently no one is currently working on the behavioral ecology of Antarctic krill. Our last underwater observations of Antarctic krill were in 1985–1986, and since then, only one investigator (O'Brien 1987*a*) has made systematic underwater observations of *E. superba*. Further, only a few laboratory investigations of euphausiids have been conducted in the last 20 years (e.g., Kils 1982; O'Brien 1988; Price 1989). Most krill research is conducted by oceanographers whose graduate education did not include the subjects of animal behavior or evolution (Hamner 1985), but ignorance of krill behavior can no longer be condoned because schooling behavior affects absolutely every aspect of the biology of krill after metamorphosis from furcilia VI (Hamner et al. 1989).

Schooling behavior of krill at sea must be placed within the context of a large body of literature on three-dimensional aggregative behavior of other schooling or flocking species (some 700 references in Parrish and Hamner 1997). Animals aggregate in complex patterns for a variety of reasons, such as protection from predators, reproduction, migratory and energetic benefits, and group foraging (Parrish and Hamner 1997; Parrish and Edelstein-Keshet 1999). Ritz (1994), in an exceptionally important review, evaluated the literature on social aggregations in pelagic invertebrates. The importance of schooling by Antarctic krill has been reviewed recently in relation to predation, cover, and convergent evolution in the Antarctic epipelagic ocean (Hamner 1995), and Folt and Burns (1999) reviewed patchiness of zooplankton, including aggregative behavior in mysids and euphausiids.

Folt and Burns (1999) contended, and we agree, that data about physical oceanographic processes must be accompanied by detailed information on the behavioral reactions of zooplankton to explain animal distribution patterns in the sea. They suggested that four biological factors — vertical diurnal migration, predator avoidance, finding food, and mating — generate most instances of zooplankton patchiness. Their review provides a useful foil for our essay on krill behavior because, like most workers in the field, they continue to refer incorrectly to euphausiids as classic swarmers, even though everyone who has watched euphausiids at sea, from Hardy and Gunther (1935) to Hamner et al. (1983) and O'Brien (1987*a*), has commented that all the individuals within these aggregations are polarized, regularly spaced, and swimming in the same direction. Polarized congregations of animals are formally assigned the word "school" in English dictionaries, and groups of animals that school are said to engage in schooling behavior. Swarms do not exhibit polarization of individuals, nearest neighbor distances in swarms are not uniform, and swarms do not travel directionally (Parrish and Hamner 1997; Parrish et al. 1997).

Hardy's description of *E. superba* swimming near a pier (Marr 1962, p. 154) is appropriate to the behavior of a school despite his use of the term "swarm": "They were all swimming hard and going round and round, sometimes in a circular course, and sometimes in a 'figure 8', but never breaking away from the one mass....I put in my walking stick and stirred the whole swarm up quickly so as to scatter them in all directions; but within half a minute they were all back again in their old formation." The distinction between swarms and schools is critical for understanding most aspects of the biology of pelagic euphausiids.

Schooling

Individuals within schools

In order to understand the significance of the social behavior of individual krill within krill schools at sea, consideration of the literature on schooling behavior is instructive. The earliest work on schooling behavior was conducted primarily with fish (reviewed by Breder 1959; Williams 1964; Radakov 1973). These initial investigations focused on emergent attributes of the school as a whole, characteristics such as size, shape, density, packing geometry, movement synchrony in space and time, sensory stimuli involved with schooling, and the adaptive significance of the behavior itself. Classically, all individuals in a school were considered to be identical in every aspect of morphology and behavior (Breder 1959; Shaw 1978). Unfortunately, this early emphasis on attributes of the school as a whole and on the uniformity of the individuals within the school intellectually constrained progress in understanding schooling behavior because it ignored the role of individuals within the aggregation, treating individuals as if they behaved altruistically for the benefit of the school as a whole. We know now, of course, that fish in schools are just as selfish as everyone else. Emergent properties of schools do not violate evolutionary theory (Hamner and Parrish 1997). The school is indeed greater than the sum of its parts even though the unit of natural selection is an individual animal (Pitcher et al. 1982; Helfman 1984; Hamner and Parrish 1997).

Individual animals are the focus of all ethological investigations. Ethological studies require that activities of individual animals be documented through space and time, but for schooling species, this has been extremely difficult, primarily because schooling is so widely employed as a visual antipredatory device (e.g., Hobson 1968; Hamner 1995; Parrish and Turchin 1997). For schooling behavior to be effective against predators, the appearance and behavior of all individuals within the school must be as similar as possible. When the collective behavior of large numbers of almost identical animals is rapid, highly coordinated, and synchronously executed, it is visually difficult to track a given individual in order to capture it. Schooling behavior therefore exploits, among other things, confusion of the optic circuitry of visual predators, particularly vertebrates. Not surprisingly, since humans have the same basic visual system as aquatic vertebrates, the schooling behavior that confuses the predator also confuses the scientist. As a consequence, many questions associated with schooling were not amenable to resolution until recently because the most important approach of modern ethology, its focus on the behavior of the individual, is exceptionally difficult to apply to schooling species. As a result, few investigations have been published that track the actual location of an individual within a school over time (Healey and Prieston 1973; Pitcher et al. 1982).

Three relatively new approaches have been exploited in an effort to understand discrete behavior of individuals within schools. In one approach, the investigator directly observes small schools or individually marked animals within small

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schools in the laboratory or in the field (e.g., Hobson 1968; Neill and Cullen 1974; Major 1978). By restricting group size or marking individuals, the investigator can follow one animal within the group, whereas larger schools are visually unmanageable because the eye simply cannot track the individuals.

Investigation of the internal dynamics of larger schools requires a second general approach using photographic, cinematographic, or videographic techniques, often with behavior of individuals in the school being analyzed with the aid of computers (e.g., Cullen et al. 1965; Hunter 1966; Parrish and Turchin 1997). Nonetheless, in even the most recent investigations with the best computers, it has been possible to document schooling behavior of individual fish only in small schools (up to 15 individuals per school) for only brief periods of time (up to 10 s) via stop-frame analysis (Parrish and Turchin 1997). This is because increasing the number of individuals in the school or the duration of tracking sequences vastly increases the amount of time and effort required to postedit the data files. Computers routinely confuse the paths of intersecting individuals, and it is neither cost effective nor emotionally rewarding to spend a month editing 10 s of data on three-dimensional movements of 15 frightened fish. Even if computers were as good as humans at distinguishing between intersecting pathways during slow-motion replay of three-dimensional footage, one could never see deeply into the forest because ultimately, trees get in the way (Osborn 1997). Most previous three-dimensional investigations of schools, flocks, and swarms have been laboratory studies, but there have been a few three-dimensional studies at sea of fish and krill (Klimley and Brown 1983; O'Brien 1987*a*, 1989).

A third general approach to analyzing behavior of animals within schools, flocks, swarms, and pods utilizes modeling and simulation (e.g., Clark and Mangel 1986; Zhou and Huntley 1996; Grünbaum 1997). But Parrish and Edelstein-Keshet (1999) noted that although many sets of simple rules can lead to lifelike group behavior, there is no guarantee that living systems follow simple rules. To understand how individual euphausiids spend their time within schools in a three-dimensional sea, we must collect three-dimensional data over time, and we must also model both schools and individuals within schools in relation to real data (Levin 1997).

The behavior of one free-swimming krill that we observed while diving in Antarctic waters drives home the importance of the behavior of an individual euphausiid within the three-dimensional structure of a small school. We released a large, solitary euphausiid from a collecting jar underwater at about 10 m depth. From a distance of about 5 m, we followed this animal as it swam rapidly away on a fixed horizontal course. After several minutes, it visually located a small school containing a few hundred krill. The lone individual veered sharply, entered the school, and immediately adjusted its swimming speed and orientation to conform with the other krill, but we could visually track this animal because all of the others in the school were much smaller. The large euphausiid swam in synchrony in the center of the school for approximately 30 s and then changed position, first to the front, then to the back, to the bottom, to the sides, and finally to the top of the school, swimming in each new location only briefly. The large euphausiid then swam upward out of the school, reoriented horizontally, and swam rapidly in a straight line away from the school. We surmise that this large individual gauged the size of its new colleagues and, finding them too small for comfort, elected to be alone in the open ocean rather than to swim with juveniles.

Size of schools

Schooling may confer many individual benefits, such as reproductive advantages or protection from predators, but schooling has concomitant disadvantages, such as competition for food and increased incidence of disease. Further, the relative evolutionary trade-offs between small and large aggregations suggest that there is some sort of optimal intermediate group size that balances these complex density-dependent interactions (Parrish and Edelstein-Keshet 1999). In large schools, for example, the absolute number of individual animals creates an internal microenvironment of waste products, reduced oxygen, parasites, disease, and lack of food that is ultimately detrimental (Pitcher 1986; Parrish and Edelstein-Keshet 1999). Because of these disadvantages, very large fish schools are extremely rare. For example, anchovy shoals off southern California average only about 15 m in diameter (Koslow 1981).

Very large krill schools probably are also relatively rare. Outlines of three sets of independent yet similarly small surface aggregations of *E. superba* are shown in Miller and Hampton (1989), and Nemoto (1983) described the long axis for Antarctic krill patches at the surface as generally less than 30 m. Surface schools that are small in at least one dimension are consistent with all reported underwater observations of school size (e.g., Ragulin 1969; Hamner et al. 1983; O'Brien 1987*b*), and there is no compelling reason why surface schools of krill (or fish) should differ categorically in size or shape from krill (or fish) schools swimming deeper. Observations of relatively small schools are in stark contrast with some acoustic records that suggest that immense, solid aggregations of krill occur in Antarctic water in "super swarms" (Macaulay et al. 1984; Shulenberger et al. 1984; see discussion in Miller and Hampton 1989). These supposedly exceptionally large swarms exceed any metric for optimal shoal size, using appropriate figures for oxygen, food depletion, or ammonia accumulation (Ritz 1994). It is simply not possible for schooling animals to survive within dense aggregations if absolute size of the shoal is too large. Supposed super swarms and seemingly endless acoustic records of krill undoubtedly will prove to be aggregations that are thin in at least one dimension (Hamner et al. 1983). Recent acoustic recordings of krill school size by Ross et al. (1996) demonstrated that school sizes of *E. superba* change in complex ways. Nonetheless, the average length of all schools for all months and years was only about 100 m, and average thickness of the schools was only about 15 m. (Ross et al. 1996). Further, these average dimensions for krill schools represent substantial overestimates because their acoustic system did not record schools shorter than 25 m, yet small schools were common (see also Miller et al. 1993).

One obvious drawback to large school size for krill, besides the ever-present problem of intraspecific competition for food, is the increased risk of epidemic infection and disease in large schools (Hamner 1984*a*). Transparent pelagic

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animals that are parasitized, damaged, or sick lose the metabolic ability to maintain tissue transparency, and they often become opaque and whitish some days before death. It is easy underwater to distinguish between healthy and apparently unhealthy *E. superba*. We regularly observed significant numbers of whitish krill within schools, often separated by a small halo of clear water from their more transparent neighbors (Hamner 1984*a*). When we deliberately herded krill schools, so that the school as a whole increased its swimming speed to avoid the divers, whitish individuals often fell behind as isolates, unable to maintain the swimming pace of the school.

To pursue this subject (W.M. Hamner and J.J. Stretch, unpublished data) we hand-collected 25 whitish krill that swam as isolates behind schools and we captured another 25 transparent krill at random from within schools as controls, without touching the krill by guiding the krill into individual 1-L jars. Krill were maintained aboard ship in these jars, with water changed gently twice a day. All 25 control animals survived in the jars for the 14 days of the experiment, but 23 of the 25 animals captured as isolates were dead within 36 h.

In a separate exercise, we hand-collected and autopsied 80 solitary krill, many of which were whitish, that we found swimming alone near or behind schools. In decreasing order, they were parasitized (Protozoa: Suctoria: *Ephelota* sp.), had molt problems (exoskeleton pieces still attached), had tumors, or were physically damaged. We collected 85 individuals as controls from within schools. None of the controls were infected, damaged, or tumorous.

Density of schools

Mauchline (1980) proposed that krill aggregate over a wide range of densities. He defined schools (individuals in parallel orientation) and swarms (individuals without parallel orientation) as aggregations with the highest local densities, 1000 – 100 000 krill·m^{-3}. In his classification scheme, shoals were an order of magnitude less dense (1–100 krill·m^{-3}), patches and breeding aggregations still less dense (1–10 krill·m^{-3}), and aggregations would contain the fewest individuals (0.1–1.0 krill·m^{-3}). Other more recent classifications are similar (Kalinowski and Witek 1985; Miller and Hampton 1989; Siegel and Kalinowski 1994). These putative types of aggregations also supposedly intergrade one into the other, yet when others and we observe live krill underwater in the Antarctic, krill are almost never krill in any type of congregation other than schools. Mauchline's (1980) behavioral definitions are not realistic.

Edges of krill schools that others and we (e.g., Ragulin 1969; Hamner 1984*a*; O'Brien 1987*b*) have seen and filmed underwater are always abrupt, with no density gradient from the outside to the inside of the school (Fig. 1) (video in Brinton et al. 1999). Density inside schools is always high, whereas outside the school, there is empty ocean. Krill schools do occasionally break up, however, and individuals do sometimes feed independently on patches of phytoplankton (Hamner et al. 1983), on ice algae growing underneath sea ice (Hamner et al. 1983; photograph by F. Nicklin in Hamner 1984*b*, p. 643; Stretch et al. 1988), on one another, and on *E. superba* molts (P.P. Hamner, personal observations). Further, krill regularly leave schools when molting (Hamner et al. 1983) and when mismatched by size with the rest of the school (Hamner et al. 1983). Nonetheless, we concur with Marr (1962) that *E. superba* is an obligate schooling species that spends its life after metamorphosis within the social context of a school. Krill have a behavioral biology like that of sardines, which also always live within the structure of schools.

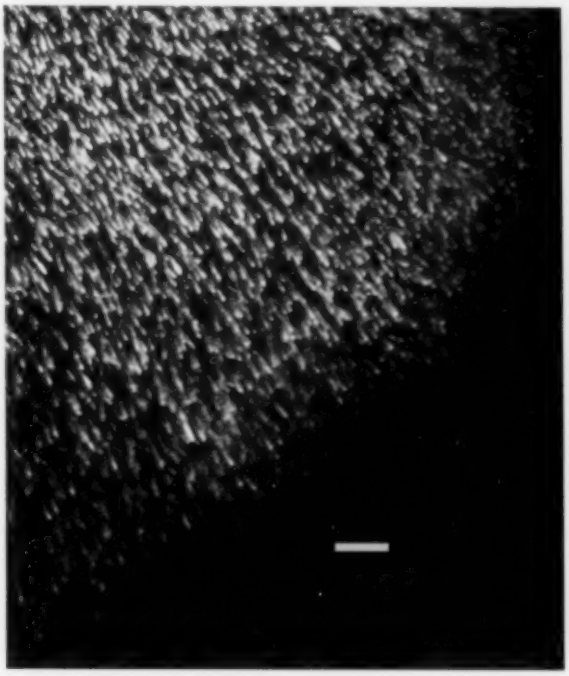

Fig. 1. School of *E. superba*. Individuals within the school are polarized, densely packed, and swimming obliquely down to the right. No krill are outside the school. Whitish individuals within the school have lost tissue transparency and will soon die. Scale bar = 10 cm.

Density and biomass estimates depend on sampling tools. These samplers fall roughly into three categories: nets, acoustics, and "other," with the last category mostly referring to photography, visual estimates, or bucket samples. All sampling methods must be calibrated for accuracy and precision. Thus, visual counts of krill by divers and by observers from small boats or docks produce relatively accurate density estimates, but repeated counts have a high variance. Consequently, visual estimates are accurate but imprecise. The earliest observers on boats and docks (Hardy and Gunther 1935; Marr 1962) visually estimated Antarctic krill density at 1 krill·in^{-3}, which translates to about 64 000·m^{-3} or 32 kg·m^{-3} for a 0.5 g wet weight *E. superba*. Later, diving scientists confirmed these densities for *E. superba* (Ragulin 1969; Hamner et al. 1983; Hamner 1984*a*) and for five other species of schooling euphausiids (Table 1).

Individual animals can be counted repeatedly in photographic images with precision, but most underwater photography is done with standard cameras, and it is impossible to determine depth of field precisely from two-dimensional images. In contrast, three-dimensional images produce both accurate and precise estimates of density, an approach that has

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Table 1. Estimated numbers and biomass of six species of euphausiids.

Species	No.·m^{-3}	Biomass (g·m^{-3})	Sampling method	Reference
E. superba	64 000	32 000[a]	Visual observation	Marr 1962
	55 000	27 500[a]	Photography	Ragulin 1969
	30 000[b]	15 000	Visual observation	Makarov et al. 1970
	25 000	12 500[a]	Photography	Hamner et al. 1983
E. lucens	480 000	10 700	Bucket	Nicol et al. 1987
E. crystallorophias	30 000	3 000[c]	Photography	O'Brien 1987*a*
E. pacifica	72 000	7 200[c]	Photography	Hanamura et al. 1984
E. vallentini	75 000	7 500[c]	Photography	Ragulin 1969
Nyctiphanes australis	480 000	10 560[d]	Photography	O'Brien 1988

[a]Biomass calculated from number of individuals assuming 0.5 g wet weight per individual.
[b]Number calculated from biomass assuming 0.5 g wet weight per individual.
[c]Biomass calculated from number of individuals assuming 0.1 g wet weight per individual.
[d]Biomass calculated from number of individuals assuming 0.022 g wet weight per individual.

been used underwater for euphausiids and mysids by O'Brien (1987*a*, 1989). Although photogrammetric techniques are exceptionally precise and absolutely accurate, they work only at short ranges for animals of the size and density of schooling krill (O'Brien 1987*a*, 1989). Ultimately, the krill themselves occlude the optical pathway (Osborn 1997; Parrish and Hamner 1997).

When BIOMASS became an international Antarctic program in the early 1980s, many of the sampling techniques and procedures associated with krill biology became codified so that research groups from different countries and institutions could compare their data (see Miller and Hampton 1989). This seemed logical at the time, but in retrospect, it did not necessarily produce good science. When everyone uses the same tools, everyone collects similar data, and although precision increases, there is no way to independently assess accuracy. For example, BIOMASS participants all began using similar nets and similar acoustic systems to determine krill densities and distributions, whereas almost no one studied net avoidance (but see Everson and Bone 1986). Nets, already well known to be biased, were then used to calibrate acoustics. Miller and Hampton (1989), in an exceptionally scholarly review, noted that "...estimates of swarm density have been made directly from visual or photographic observations.... With the exception of Guzman and Marin's (1983) photographic estimates...all [of the visual] estimates...exceed acoustically-derived values by at least two orders of magnitude." Unfortunately, Miller and Hampton (1989) concluded incorrectly that "...it seems highly unlikely that swarm densities in the region of 10 kg·m^{-3} could be typical, as this would imply errors of two orders of magnitude in practically all available acoustic estimates of density." But O'Brien's (1989) photogrammetric data cannot be incorrect. Densities of krill in schools in eight other investigations were also higher than nets or acoustics by two orders of magnitude (Table 1).

We reexamined the Guzman and Marin (1983) paper. It is clear from the diagram of their drop camera within its protective frame (which projected about 0.3 m in front of the lens), from the depth of field (0.5–2.0 m) and from the disorientation of krill close to the camera, that the camera penetrated into polarized krill schools but only scattered the krill closest to the lens. Similarly, we could approach schools underwater only to about 1.5 m from the side without disturbing the animals (Hamner et al. 1983, 1984*a*; confirmed by O'Brien 1987*a*). Guzman and Marin (1983) noted that "In spite...of time, depth...the attitude of krill is very similar, with all specimens gathered swimming with the same corporal orientation." Their 700 images support the occurrence of krill in schools at exceptionally high densities over a wide geographic area.

Patchiness of zooplankton, of course, has generated interpretive controversy for more than 100 years. Ernst Haeckel (1890) took vigorous issue with Victor Henson's preoccupation with average densities of zooplankton, stating that Henson's averages were not only spurious but also perverted because they "...arouse a deceptive semblance of mathematical accuracy." Brodie et al. (1978), in a charming contribution on the feeding biology of fin whales off Nova Scotia, noted that average densities of euphausiids estimated via nets and acoustics were insufficient to feed fin whales. They calculated that the whales would need to swim at speeds of 900 km·h^{-1} to fill their stomachs in 8 h on average densities of euphausiids.

Krill schools are regularly arranged internally, with characteristic nearest neighbor distances and densities and with extreme polarization of the individuals within the school (O'Brien 1989). The schools themselves are patchy in distribution and variable in size and shape. Underwater, we have seen many schools no larger than a beach ball (Hamner et al. 1983; Hamner 1984*b*), whereas other schools have been as large as the surface schools described 60 years ago by Hardy and Gunther (1935). On one dive, we saw hundreds of schools of krill, of every conceivable configuration except a solid mass, coursing in different directions, changing depths, coalescing, and separating. A ship passing over such an aggregation probably would have recorded acoustically these complex aggregations as a single solid patch of krill (e.g., Macaulay et al. 1984), yet animals in the center of the schools were never far from the perimeter. It is encouraging that some of those investigators who rely on acoustics now contend that "Krill normally have a tendency to form small, more compact swarms" (from Siegel and Kalinowski 1994; Watkins et al. 1986).

Clarification of how schooling behavior of Antarctic krill is initiated is important because it demonstrates that schooling can be manipulated experimentally. We observed schooling behavior in *E. superba* in the laboratory in large circular tanks at Palmer Station, Antarctica. We demonstrated fright responses of krill in these tanks to krill-Schreckstoff, aver-

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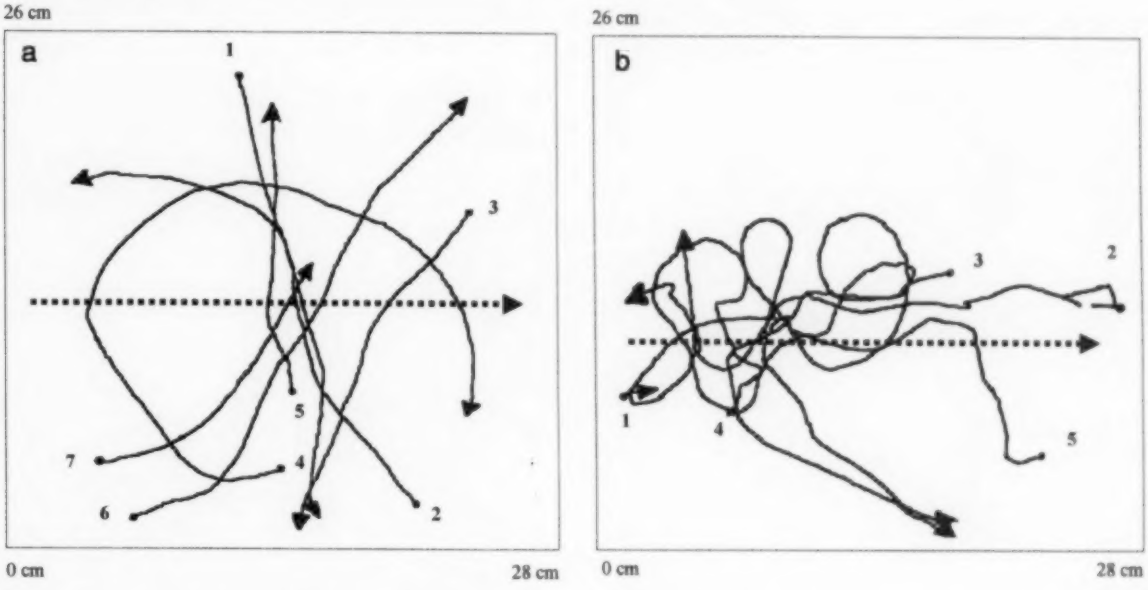
Fig. 2. Tracks of individual krill swimming in a shallow flume with laminar flow from left to right. (*a*) Krill show no response to trails of fluorescein dyed seawater. (*b*) Krill respond with area-intensive turning and more rapid compression-filtration to 5% Newcastle Ale introduced into the flow.



sion responses to dilute solutions of ammonia and urine, and reaggregation responses to varying light levels and models of predators (Strand and Hamner 1990). Further experiments are badly needed to elicit information about the formation and maintenance of krill schools.

Foraging

Under certain circumstances, such as when foraging intensively within a patch of food, molting, or mating, krill abandon the school and behave individualistically. At Palmer Station, we observed area intensive foraging behavior by krill in patches of phytoplankton in aquariums, and subsequently, Price (1989), in an elegant experiment, used three-dimensional optics and a 10-m-high tower tank to document area-intensive foraging behavior by *Thysanoessa rashii* in response to a phytoplankton patch.

In experiments to learn how krill locate food, we demonstrated that tethered krill used chemoreception to detect low levels of amino acids (Hamner et al. 1983). Subsequently (W.M. Hamner, unpublished data), we studied scent tracking by free-swimming krill in a flume (1 × 2.5 m) with flows of 1–3 cm·s^{-1}. Shallow water, 4 cm deep, in the flume constrained swimming to two dimensions. Pencil-thin fluorescein dye trails confirmed laminar flow in the flume. Odors added to the dye trail created fluorescent scent trails. We tested attractive chemicals shown earlier to elicit chemoreception (Hamner et al. 1983), such as phytoplankton odors, dilute amino acids, and 5% Newcastle Ale. For each experiment, we placed krill that had not fed for 24 h into the flume for 5 min before introducing odors or before running controls without odors. Behavior of individuals was recorded by an overhead video camera and the images were subsequently digitized and analyzed by an Expert Vision motion analysis device, as described by Hamner and Hamner (1993).

Of the 23 different experiments that we conducted, we have analyzed only one for this review. Krill showed no response to the control dye trail (Fig. 2*a*), but when we added attractive odors to the seawater in the fluorescent trail (Newcastle Ale in this particular experiment), they engaged in more rapid compression-filtration with the thoracic appendages and in localized turns through the odor plume (Fig. 2*b*). Although excited animals attempted to track the scent trail at high speed to its source, most of the krill lost contact with the scent trail because they swam so fast. However, many relocated the scent trail and some individuals even fed stubbornly from the tip of the delivery pipette. Foraging behavior of free-swimming krill therefore appears to involve distance chemoreception, directional tracking behavior, and area-intensive foraging.

Successful feeding requires that animals mechanically harvest and handle food once it is found, and investigations of foraging require accurate knowledge of the morphology and function of the feeding appendages. Accordingly, we reexamined the structure and function of the feeding basket of *E. superba* (Hamner et al. 1983; Hamner 1988). We used high-speed cinematography, fluorescent dye, and carmine and phytoplankton particles in conjunction with anatomical studies to determine how the thoracic appendages of euphausiids function during filter feeding. We confirmed the superb morphological work of Zimmer (1913) and Barkley (1940), who postulated that water and phytoplankton enter the feeding basket from the front and that water is squeezed out laterally through the filter setae via compression-filtration. As water is strained through the setae, phytoplankton remains inside the filter basket and is raked forward by the comb setae to the mouth (Fig. 3) (Hamner 1988).

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Fig. 3. Individual *E. superba* with six pairs of thoracic appendages extended prior to closure during a bout of compression filter feeding. Scale bar = 1 cm.

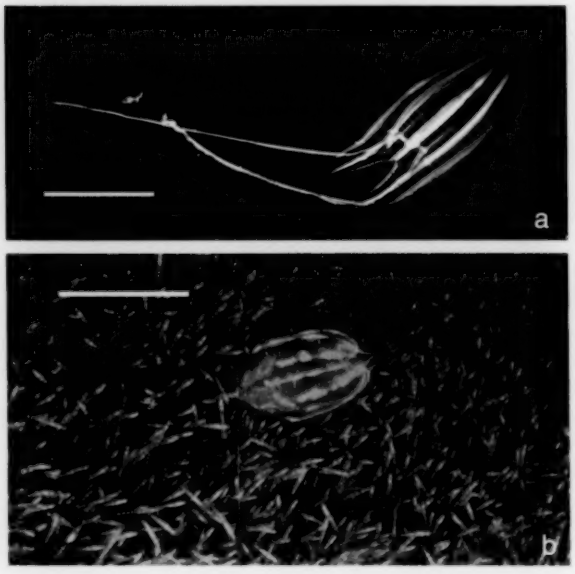
We produced a 16-mm movie on feeding and swimming behavior of Antarctic krill (University of California Extension Media 1983) that shows krill utilizing a variety of filtration and foraging patterns depending on the density and location of phytoplankton and the type of food available. In addition to compression-filtration, krill use the extended thoracic appendages as scraping tines to harvest floating material from the sea surface, to graze on benthic materials, and to hold and eat molts and krill carcasses. Krill also rake ice algae off ice surfaces with the carpus, propodus, and dactyls when the legs are fully extended (Hamner et al. 1983; Hamner 1984*a*). Krill were filmed filling the feeding basket completely with ice algae, packing it into a bolus, and sequestering this ball of food. Krill carrying food boluses swam away from hungry colleagues. Krill fought over and stole food balls from one another.

Ice algae feeding by krill was initially observed in the laboratory at Palmer Station (Hamner et al. 1983; Hamner 1984*b*), but divers have subsequently observed feeding on ice algae in the sea (e.g., O'Brien 1987*a*; Marschall 1988; Stretch et al. 1988). Ice algae occur only near the sea surface, so we examined how *E. superba* find ice algae in laboratory experiments. We first constructed vertical scent trails by dropping dyed food into the aquarium to see if krill would track scent trails downward to a food source as does *Acetes sibogae* (Hamner and Hamner 1977), but in contrast to *A. sibogae*, which swims down vertical scent trails at high speed, *E. superba* failed to track vertical trails downward to the food, although it was clear from their increased turning rates that the krill perceived the chemicals in the scent trails. We then floated ice blocks containing ice algae in the aquarium, and melting ice released vertically sinking salt fingers enriched with ice algae. Krill swimming below the ice located these fingers, began area-intensive foraging, and increased their compression-filtration rates. As they circled, the krill gradually rose upward to the ice block, where they switched from compression-filtration to scraping behavior with extended thoracic legs (see video in Brinton et al. 1999).

Antipredatory behavior

Little has been written about antipredatory behavior of krill, but we note that schooling of krill is a generalized antipredatory behavior that deters, on average, all krill predators (Hamner 1995). We report here new observations, both in situ and using planktonkreisels (a plankton aquarium, Hamner 1990), on how the large cydippid ctenophore *Callianira antarctica* captures krill and how antipredatory

Fig. 4. Cydippid ctenophore *C. antarctica* (*a*) in clear water, with tentacles extended in fishing mode, with one *E. superba* captured (scale bar = 10 cm) and (*b*) in the midst of a dense school of krill, with tentacles completely retracted (scale bar = 20 cm). The organization of krill in the school has been somewhat disrupted by the proximity of the photographer.



behavior of krill helps krill escape sometimes from tentaculate predators. At sea, we saw individual ctenophores with feeding tentacles fully extended, often with partly digested krill in their guts (Fig. 4*a*), but only where there were no krill schools in the immediate vicinity. Schools obviously had been present previously, as evidenced by patchy acoustic records of krill on the ship's echosounder and by the presence of isolated damaged krill, krill fecal pellets, and molts in the water column around the ctenophores. In contrast, when *C. antarctica* did occur simultaneously with dense schools of krill, the ctenophore guts were empty and the fishing tentacles were completely retracted (Fig. 4*b*). We have many video sequences from the laboratory and numerous still photographs taken at sea that illustrate this relationship.

Callianira antarctica, like all cydippid ctenophores, captures individual prey with sticky colloblasts and fishes the prey with one of its two stretchy tentacles like a fisherman playing a fish. Eventually the ctenophore retracts the tentacle with attached prey toward the tentacle sheath, but the tentacle sheaths are lateral to the mouth and the ctenophore must roll sideways toward the prey while simultaneously relaxing the tentacle in order to bring the prey to the oral lips. These mechanical problems limit prey capture to one item at a time.

Once captured by *C. antarctica*, krill often escape. In laboratory plankton kreisels, we have seen four distinctive, sequential antipredatory behavior responses of krill to this particular ambush predator. The first response by a euphausiid to discharge of colloblasts is a multiple tail-flip reaction that often results in escape by dislodging or tearing apart the

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tentacle, followed by grooming to remove tentacle fragments. If an initial lobster tail escape response is ineffective, the ensnared euphausiid exhibits a second antipredatory behavior that involves steady swimming with the pleopods at high speed directly away from the ctenophore. Sometimes this is effective because the ctenophore cannot contract its tentacles to complete its feeding maneuvers when it is being dragged along by the krill. Tension exerted by the krill on the stretched tentacle often exceeds the contractile strength of the tentacle, and therefore, sustained, directional, strong swimming by the krill often results in its release.

If steady swimming does not dislodge the ctenophore, a third antipredatory behavior is exhibited wherein the krill plays dead and passively sinks, using its weight to cause tentacle extension and tentacle fatigue. If the euphausiid is too heavy, the ctenophore cannot roll quickly enough to bring the prey to the lips before the weight of the krill causes it to sink once again. Then the ctenophore must repeat the entire handling sequence anew, swimming upward, stretching the tentacle, retracting the tentacle toward the tentacle sheath, and then relaxing the tentacle just prior to the feeding roll. If the ctenophore makes repeated abortive attempts to bring the prey to its mouth, eventually the colloblasts will release their grip and the krill will sink free, whereon it immediately reorients and swims away horizontally. The lips of the mouth, however, eventually grasp some captured krill. When this happens, the euphausiid switches instantly from total inactivity to repeated violent tail flipping, twisting, and frantic grooming in a last effort to escape. Sometimes this fourth behavior is successful and the krill escapes, but more often the krill is exhausted and held firmly by the lips. Then, both the fishing tentacle and the prey are drawn into the pharynx, the tentacle releases the krill and drops away, and the ingested krill continues into the stomach.

It is often difficult to demonstrate the relative adaptive merits of any given behavior, but in the presence of predatory cydippid ctenophores such as *C. antarctica*, the advantage of schooling behavior of krill is clear. Schooling protects krill from *C. antarctica* via mechanical damage to the ctenophore's tentacles. It is impossible for cydippid ctenophores to capture one krill at a time within a school because their extended tentacles would be tangled and torn off. Because krill are reasonably rare outside schools and because ctenophores cannot capture krill within schools, it is probable that ctenophores are not their dominant predator. Ctenophores are, nonetheless, interesting predators from behavioral and evolutionary points of view. Everything in oceanography need not be rationalized in terms of ecological impact.

Each species of krill predator finds and feeds on krill in unique species-specific ways, whereas krill always live within schools and they must rely on schooling as a generalized antipredatory behavior that deters, on evolutionary average, all of the predators that eat krill. Krill do exhibit some unique and complex antipredatory escape behaviors in response to tactile predators such as *C. antarctica*, and instantaneous molting is an antipredatory decoy for visual predators (Hamner et al. 1983; Buchholz et al. 1996). Nonetheless, schooling is the primary collective defense for krill against predators. Although every species of predator feeds in unique ways, krill predators can be broadly categorized into those that capture krill individually and those that are batch feeders. Penguins feed on isolated krill one at a time, whereas baleen whales are of necessity batch feeders that cannot be sustained by thinly distributed resources (Brodie et al. 1978). To our knowledge, no one has published direct observations of underwater predation by any visual predator on Antarctic krill in the open sea or of baleen whales feeding at depth on krill. The antipredatory response of krill to batch feeders presently must be inferred indirectly from the response of krill schools to divers (Hamner et al. 1983; Hamner 1984*b*; O'Brien 1987*a*), to nets (Shust 1969; Everson and Bone 1986), or to other large, fast-moving objects.

We deployed a Diver Transport Vehicle (DTV) in Charlotte Bay, Antarctica, in 1984–1985 to increase our horizontal search area to locate schools of krill. This vehicle, which can be considered a "large, fast-moving object," was a towed, wet submersible, 1 m high × 2 m wide × 3 m long, that carried two scuba divers in a prone position. The front of the DTV was a clear Plexiglas dome, providing excellent visibility. The towline attached to the top of the vehicle and did not obstruct visibility, yet it always could be seen above and in front of the vehicle by the divers when under tow. The DTV was highly maneuverable under tow at speeds of approximately 4 kn, and we located krill schools every time we used the wet sub. Our longest transect underwater before intercepting a krill school was about 2 km. Generally, upon locating a krill school, the towline was released, the divers exited the DTV, the vehicle floated to the surface, and the divers approached the krill school more slowly.

On many occasions, the DTV was towed through the center of a school of krill. If the vehicle entered the school slowly, at about 1 kn, the krill simply moved horizontally away from the towline and away from the vehicle, creating a 1- to 2-m-wide vertical swath of clear water from the surface down to and around the towline, an avoidance pattern identical to those described by Marr (1962) and illustrated by Shust (1969) for surface schools of krill avoiding nets. The DTV itself produced a long, horizontal hole devoid of krill after it passed through a krill school, like the halo of empty water around nets, as drawn by Shust (1969).

If the vehicle entered a school rapidly (2–4 kn), the krill tail-flipped backward randomly away from the vehicle (Hamner et al. 1983; Hamner 1984*a*; O'Brien 1987*b*). Most of these krill successfully avoided the DTV, but krill do not move in straight lines while tail-flipping and some managed to tail-flip in front of and into the DTV through the air exhaust vents. This reaction to the DTV as it plunged into the school appears similar to the behavior exhibited by krill when a net is pulled rapidly through a school, and we believe that krill are caught by midwater trawls because they panic and tail-flip accidentally into the net, whereas the bulk of the school simply veers to the sides and avoids capture entirely. It is not surprising that batch feeders like baleen whales use complex feeding tactics to capture krill (Hamner 1984*a*), and it is also not surprising that krill densities vary so wildly when estimated from net samples.

Conclusions

Antarctic krill are behaviorally complex, highly social crustaceans that spend most of their life swimming horizontally within densely packed, highly polarized schools. His-

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torically, biological oceanographers sampled krill using plankton nets and small midwater trawls. These nets capture small zooplankton effectively, but as animals increase in size, swimming speed increases, individual behavioral patterns begin to dominate their distribution in the water column, and net avoidance increases dramatically. In the past, krill were categorized as zooplankton, but systematic underwater observations of krill during the past 20 years have shown that krill are exceptionally strong, horizontal swimmers and that *E. superba*, the largest species of krill, is an obligatory schooling species behaviorally similar to clupeid fishes. Antarctic krill are therefore nektonic rather than planktonic, and their behavioral ecology must be investigated with the same sampling methodologies used to study the behavior of schooling fish, including long-term underwater observations in space and time. During the past 20 years, diving scientists, underwater camera systems, and aquarium investigations have produced a substantial body of systematic underwater observations on the behavioral ecology of Antarctic krill, but it is important to emphasize that a complete ethological investigation of Antarctic krill has not yet been conducted. Ethological investigations require thousands of hours of observation of undisturbed, individual animals in the field or at sea, and our knowledge of the behavioral repertoire of *E. superba* is still incomplete.

We know now that *E. superba* is an obligatory schooling species and that the social behavior of krill within schools has important implications for all aspects of its biology. Juvenile krill begin to school when they reach body lengths of about 10 mm, after metamorphosis from furcilia VI. Thereafter, krill do not leave the structure of the school, apparently even at night, except to molt, mate, release eggs, or forage individually on localized phytoplankton patches or ice algae. There is no cover in the open sea, and it is exceptionally dangerous to leave the safety of the school. Nonetheless, it is important to recognize that schooling is a generalized antipredatory behavior pattern that deters, on evolutionary average, all krill predators, even though schooling does not deter all species of predators equally. Schooling is particularly advantageous against visual plankton-pickers, and it also provides excellent protection from tentaculate predators. However, schooling also has its disadvantages, as baleen whales feed most efficiently on concentrated patches of prey, and high density of krill in schools promotes parasites and disease.

Schooling behavior of krill has important implications for evaluation of previous estimates of krill density and biomass. When krill are captured by nets, density estimates are invariably 1.5–2 orders of magnitude lower than visual or photographic estimates because nets fish empty water between schools and because krill schools avoid nets. Most prior biomass estimates of krill obtained via acoustic techniques are also incorrect because acoustic target strength of krill has never been calibrated against a school of live krill of known density, size, and shape. Consequently, most biomass calculations for Antarctic krill probably are wrong because of net avoidance, empty water between krill schools, and inaccurate acoustic calibration.

Future behavioral research on Antarctic and other species of krill will require much more observational research, both in situ and in laboratory aquaria, before the entire behavioral repertoire of krill is fully described. This will involve more in situ observations by diving scientists as well as extensive use of remote, underwater cameras. Underwater behavioral experiments, observations of marked individuals, and observations of krill behavior at night, at depth, and in the presence of other species of competitors or predators would be particularly instructive. Correct estimates of biomass of Antarctic krill could be made simply by recalibrating prior acoustic records using photogrammetric data for density of krill within schools.

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David I. Gibson

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L.S. Parsons and/et W.H. Lear
(*Editors/Directeurs scientifiques*)

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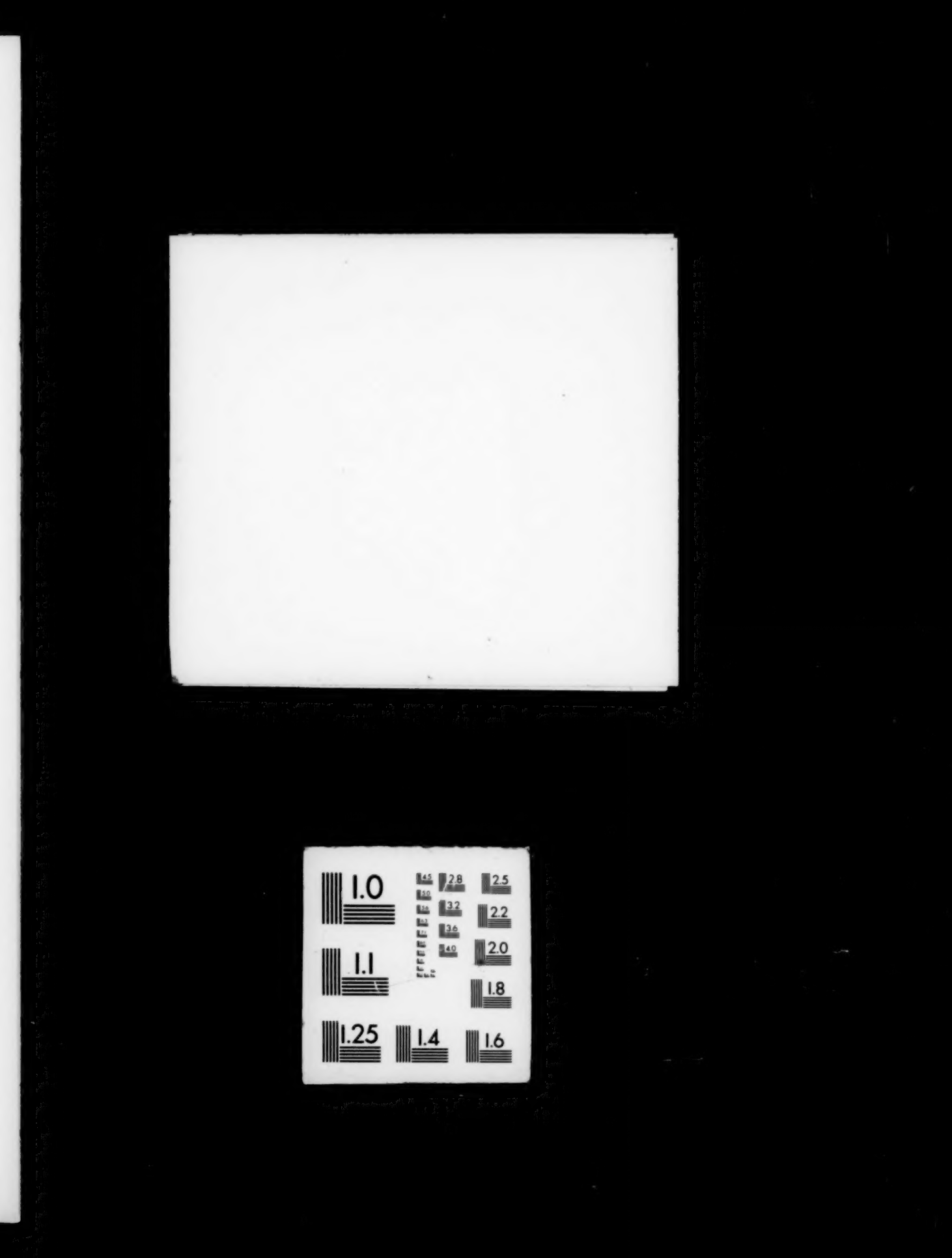
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